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BULLETIN OF THE TORREY BOTANICAL CLUB
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MATERIALS FOR A DICTIONARY OF BOTANICAL TERMS— III. INFLORESCENCES

H. W. RICKETT

Thus far in these notes[1] I have treated one term at a time, attempting to trace its introduction into botany and the changes of meaning which it has undergone at the hands of botanists. This plan will not work for the terminology of inflorescences. They have long been classified in two groups called "indeterminate" (indefinite, racemose) and "determinate" (definite, cymose); and to each of these terms a number of others are subordinate. Since the definitions of many terms thus stand or fall together, it is necessary first to discuss this classification. Nor will current usage provide a sure guide to a proper terminology, as I believe it will for other terms; for current usage, at least in English, is both confused and inaccurate.

The history of the terminology of inflorescence has been previously reviewed in some detail.[2] It suffices here first to substantiate the statements made in the preceding paragraph, and second to suggest a direction in which a solution of the problem may be sought.

Current usage may be assayed by examination of current textbooks as well as of the manuals of systematic botany in which one usually looks for morphological definitions. In addition to works previously cited in this series, the following representative texts have been used. Other works to which reference is made below are listed in the review already mentioned; there is no need to repeat the citations here.

FT: Fuller, Harry J. & Tippo, Oswald. College Botany. Rev. ed. i-xiv, 1-933. 1954.

RDG: Gibbs, R. Darnley. Botany. An evolutionary approach. i-xiii, 1-554. 1950.

HOP: Hill, J. Ben, Overholts, Lee O. & Popp, Henry W. Botany. A textbook for colleges. ed. 2. i-xvi, 1-710. 1950.

SGJ: Jones, S. G. Introduction to floral mechanism. i-xi, 1-274. 1939.

N: Northen, Henry J. Introductory plant science. i-vi, 1-601. 1953.

RP: Pool, Raymond J. Flowers and flowering plants. ed. 2. i-xxiii, 1-428. 1941.

RW: Robbins, Wilfred W. & Weier, T. Elliot. Botany. An introduction to plant science. i-vii, 1-480. 1950.

[1] Bull. Torrey Club 81: 1–15, 188–198. 1954.
[2] Bot. Rev. 10: 187–231. 1944.

[THE BULLETIN for September–October, 1955 (82: 325–418) was issued October 11, 1955.]

WIS: Smith, Gilbert M. *et al.* A textbook of general botany. ed. 5. i-x, 1-605. 1953.

TST: Transeau, E. N., Sampson, H. C. & Tiffany, L. H. Textbook of botany. Rev. ed. i-xi, 1-817. 1953.

Practically every textbook of elementary botany and every current regional manual in the English language insist on the division of inflorescences into the two types mentioned above: indeterminate or racemose and determinate or cymose. The treatment in the most-used textbooks is uniform and is obviously descended from that of Asa Gray (for which see below). The following extract is representative of the explanations being furnished to students in American colleges.

In indeterminate inflorescences "the tip of the main axis continues to grow, forming new bracts and flowers in succession as it does so, so that there occurs a rather indefinite succession of flowers . . ." In determinate types, "which are much less common than indeterminate inflorescences, the tip of the axis ceases growth very early, the meristematic tissue of the apex being used up in the formation of an apical flower. Other flowers develop laterally farther down on the axis of the inflorescence, the youngest flowers being those farthest from the apex. . . ." (FT). numerous examples are given of the former type, including snapdragon, hyacinth, stock, foxglove for the raceme, plantain, cat-tail, mullein for spike, cherry and candy-tuft for corymb; examples of the latter type are crabapple, phlox, forget-me-not.

Almost exactly the same definitions appear in other popular works (RW, RP, N); the word cyme may be substituted for the entire class of determinate inflorescences. One treatment of the cyme, after a detailed exposition of raceme, spike, corymb, umbel, etc., reads simply: "The reverse [order of flowering] is true in the type of inflorescence called a cyme. Here upward growth of the main axis is terminated by development of the entire apical meristem into a flower. The relationships between pedicels and peduncle of a cyme may be similar to that in racemes or in umbels" (WIS); and that is all! It is easy to see that the authors of textbooks regard the cymose inflorescence as much less important than the racemose. The order of flowering is omitted by RDG, HOP, who characterize the indeterminate group as having axillary flowers and the determinate as having terminal flowers. Apparently TST are the authors of the only current American textbook to omit the distinction altogether.

In the glossaries of taxonomic manuals the words "determinate" and "indeterminate" do not usually occur except incidentally; definitions must be sought under "raceme" and "cyme." The latter is commonly said to mean a broad, more or less flat inflorescence, "with its central or terminal flowers blooming earliest" (AR, LHB, MLF, GL). BDJ has a somewhat broader idea, "a flower-cluster of determinate or centrifugal type, *espec-*

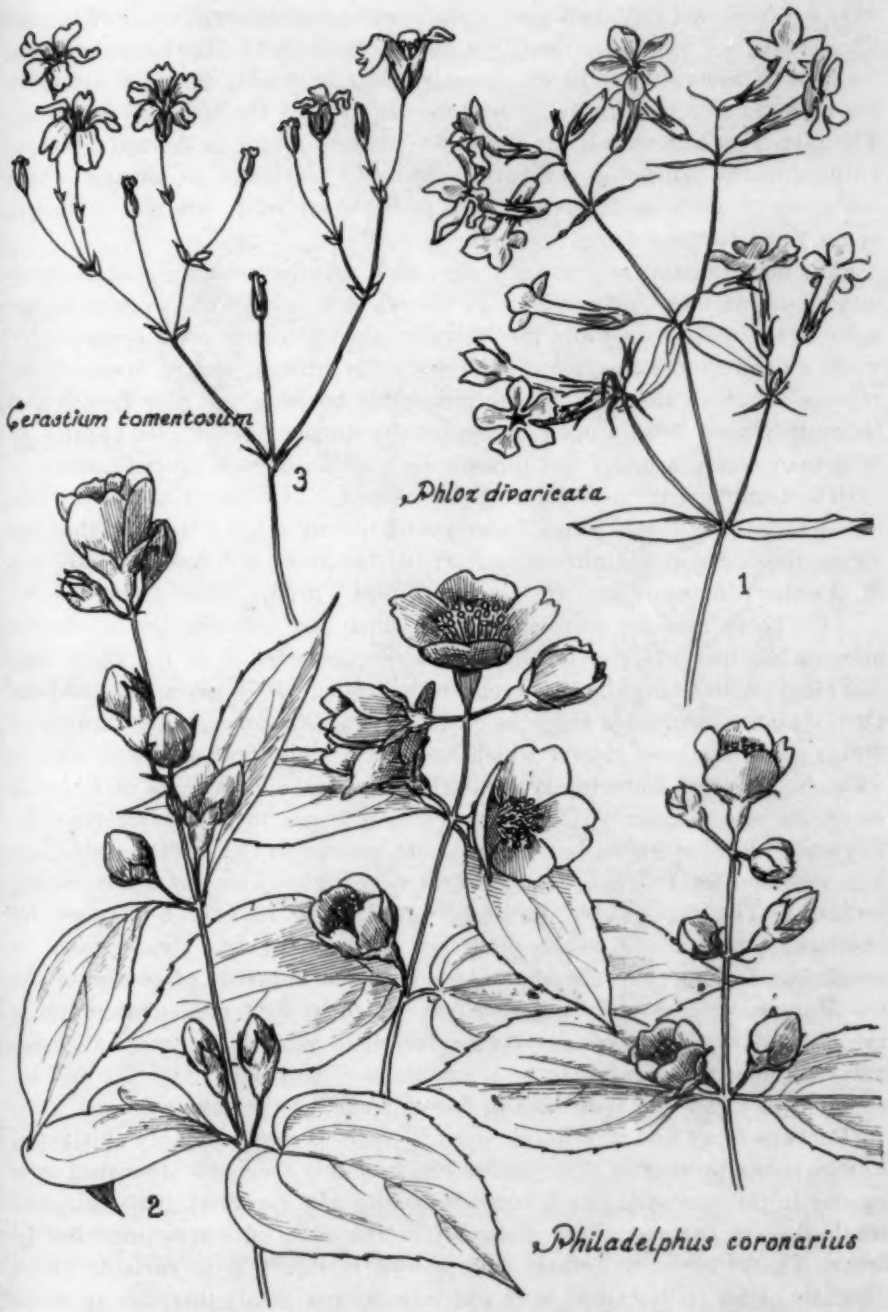


FIG. 1. Inflorescence of *Phlox divaricata:* dichasia loosely collected in a panicle. FIG. 2. Flowering branches of *Philadelphus coronarius.* FIG. 3. Compound dichasium of *Cerastium tomentosum.*

ially a broad and flattened one" (italic mine); "determinate," of an inflorescence, is "when it ends with a bud, as in cymes." HAG has for cyme "a type of inflorescence in which each flower is strictly terminal either to the main axis or to a branch," with no mention of the order of flowering. The raceme, which stands for the indeterminate group, is defined by these authors in the same way as by the writers of textbooks, as an axis which continues to grow and produce new pedicels laterally, the oldest flowers being those farthest from the apex.

We may summarize current usage, then, by characterizing an indeterminate or racemose inflorescence as one which can continue growth at the apex of the main axis while the laterally placed flowers open acropetally; while a determinate or cymose inflorescence is either a sort of upside-down raceme in which the apex of the main axis becomes the first flower and laterally placed flowers open in basipetal sequence—or, if you happen to be a taxonomist, a broad flat inflorescence which flowers centrifugally.

The trouble with these concepts is twofold: (1) most of the definitions of "determinate" and "cyme" correspond to only a few plants, so that the terms, thus defined, are almost useless; (2) too many inflorescences will not fit in either "determinate" or "indeterminate" group, as these are defined.

(1) There may be some species in which the inflorescence is shaped more or less like a raceme but flowers in reverse order; I do not know any. Asa Gray, with whom the idea seems to have originated, gives no examples. Of the plants mentioned above as exemplifying this concept, the flowers of *Malus* grow in a loose cluster which has no resemblance to a raceme and in which no order of flowering is regularly discernible. No species of *Phlox* is identified as an example; the genus certainly seems to be characterized by "cymose" inflorescences, but these do not answer to the quoted definition. The specimen of *P. divaricata* illustrated in figure 1 seems fairly representative. The flowers are arranged in dichasia (mostly 2-flowered by abortion), these being loosely collected in more or less "racemose" or paniculate fashion; there seems to be no obvious sequence of blooming. As for *Myosotis* (fig. 8), the inflorescence, which at first glance simulates a raceme and which has usually been referred to as such in American manuals, has long been known to be a cincinnus ("scorpioid cyme"); and by no flight of fancy can it be said to flower from the tip downward.

Perhaps Gray had in mind some such plant as the commonly cultivated *Philadelphus coronarius*. The inflorescence of this species is described as a raceme in the manuals; but it consists usually of a terminal dichasium and single flowers (or sometimes dichasia) in the axils of leaves immediately below. The order of flowering, as is shown in figure 2, is variable (in a previous paper[3] I described it as prevailingly basipetal; this was an over-

[3] Am. Midl. Nat. 31: 759–762. 1944.

simplification). The terminal flower almost always opens first; then the axillary flowers, in various sequences; and (usually) last of all, the two lateral

FIG. 4. Cyme of *Sambucus canadensis;* slightly simplified (but not falsified) by omitting some flowers. One terminal cluster is shown separately. FIG. 5. Raceme of *Rubus allegheniensis* (*Virginius H. Chase 12662* in Herb. N. Y. Bot. Gard.).

flowers of the terminal dichasium. Occasional branches on which the terminal dichasium is reduced to a single flower, and on which several of the

upper leaves are reduced to bracts, may simulate a raceme flowering from the tip down. Gray and others gave "chickweed" as an example of their "upside-down raceme." I have searched in vain for a specimen of *Stellaria* or *Cerastium* which would fit Gray's figure; i.e., in which the flowering would be basipetal *below the terminal dichasium*. The Caryophyllaceae are well known for their dichasial inflorescences, and figure 3 represents what is typical of the "chickweeds."

The other definition, that given for "cyme" in current manuals, is essentially Linnaeus' concept contaminated with Link's and Roeper's idea of centrifugal flowering. Linnaeus applied the word *cyma* to the inflorescences of *Viburnum, Cornus,* and the like: broad, more or less flat-topped compound clusters of many flowers. In this sense the word is still valuable. But in such clusters there is no such regular order of flowering as that specified by the authors cited above. The many branches of such an inflorescence terminate in single flowers or in dichasia (with or without abortive flowers). In a single dichasium it may well be that the terminal or central flower opens first and is followed by the two lateral flowers (fig. 4). But the several dichasia of a large group do not open in regular sequence; and, even if they did, the terminal flowers of lateral dichasia might open before the lateral flowers of more centrally situated dichasia, so that no simple sequence could be stated for all the flowers of the inflorescence. Actually the flowers of a cyme of *Viburnum* open very nearly simultaneously. The same is often true of *Sambucus;* but on some plants the marginal branches open before the central, although in each individual dichasium the terminal flower usually opens first (fig. 4). Only when a compound dichasium passes over into several cincinni which arise nearly from the same point, as in some species of *Sedum* (fig. 9), do we find a flat-topped inflorescence which blooms centrifugally.

(2) Not only do such inflorescences show that the current definitions of cymes and of determinate inflorescences do not apply to the plants supposed to exemplify them, they illustrate the second of the difficulties mentioned above: they are neither determinate nor indeterminate as those terms are currently treated. The cymes of *Viburnum, Sambucus, Cornus, Hydrangea* may be terminated in their development by an apical flower, and may be "determinate" in this sense; but they are not centrifugal unless one considers each branchlet separately, and not always then.

Still more difficult to fit into current definitions is the raceme with a terminal flower. In some of these the terminal flower is the first to open and is followed by the flower farthest from it, the remaining flowers opening in the usual acropetal sequence. Well-known examples of this are species of *Rubus* (fig. 5) and *Campanula;*[4] many branches of *Philadelphus* (fig. 2)

[4] See Goebel, *Blüthenbildung und Sprossgestaltung (Anthokladien und Infloreszenzen)*, fig. 55 (1931).

flower in this sequence. Terminal flowers are found also on the racemes of *Camassia, Convallaria, Berberis, Mitella, Ribes aureus, Dicentra, Corydalis, Prunus serotina, Robinia pseudoacacia,* and doubtless many others. Perhaps they are not all truly terminal, in the sense of "using up" the apical meristem; but SGJ's figure 4 shows a strictly terminal flower in a raceme of *Campanula.* And, in any case, this is beside the point; the growth of the axis is ended when they are formed.

In a raceme of *Corydalis sempervirens* the terminal flower may open before those immediately below it; and typical dichasia sometimes spring from the axils of the upper foliage leaves, flowering later than the raceme proper. In *Prunus serotina* and *Robinia pseudoacacia* flowering is almost or quite simultaneous throughout the raceme.

Umbels are classified as "racemose," yet the growth of their axis is usually terminated by a flower.

It is also impossible to classify, under prevailing definitions, the inflorescences of many of the Crassulaceae (to name but one family) which are terminated not by a flower but by the abortion of a flower and a resulting "false dichotomy" of the axis.

The foregoing facts lead to three conclusions.

(1) Such definitions as those of HOP, RDG, HAG merely becloud the issue; for all flowers are strictly terminal structures. Every flower "uses up" the apical meristem of a stem, whether this be the main axis or a lateral branch.

(2) Since many "racemose" inflorescences have a terminal flower and many "cymose" inflorescences have none, the presence or absence of a terminal flower on the main axis is not a safe criterion for the separation of the two groups.

(3) The order of flowering is usually but not necessarily acropetal in a raceme. The order of flowering is typically basipetal or centrifugal in a single three-flowered dichasium, but not in an inflorescence made up of many such units. In many compound inflorescences no regular sequence of flowering is to be seen.

What then becomes of the classification into "racemose" and "cymose"? Must it be abandoned, as by TST? The distinctions so glibly repeated by successive compilers of textbooks and manuals, distinctions which have their origins in botanical philosophies of the 18th century, reveal a surprising lack of attention to the discussions and controversies over these very points which exercised European botanists during the latter half of the 19th century. A brief survey of their ideas will clarify the points at issue and indicate a possible solution of the difficulties in our way.

The order of flowering was introduced into the terminology of inflorescence by Link in 1798 and developed by Roeper in 1826; in their writings

we find terms equivalent to "determinate" and "indeterminate." These were adopted by de Candolle in 1827 and by Payer in 1857,[5] without significant change. The authors of modern textbooks would feel quite at home in these ancient ones.

In 1869, however, Hofmeister was writing of cymose or centrifugal systems of branching (in general, not only inflorescences) as characterized by lateral branches which exceed the axis from which they spring; they were called centrifugal because of the termination of the branches of each successive order farther and farther from the tip of the original axis. But in an inflorescence such definitions do not hold. The branches of an umbel or corymb, which are not usually considered cymose, may equal or exceed the main axis; many cymes have lateral branches which do not equal or exceed the axis of next lower rank; and the termination of growth by the formation of flowers does not necessarily occur in the same order as the opening of the flowers.

Nevertheless the separation of inflorescences into two groups by the relative development of axis and branches was widely adopted in Germany. We find it in Sachs' famous *Lehrbuch* of 1868; he also applied the terms monopodial and sympodial to racemose and cymose branching respectively. Twenty years later Pax used the same concept, speaking of the "Übergipfelung," overtopping, of the main axis in the cymose type; he also relied on the relative degree of branching of main and lateral axes (in a raceme the main axis bears many branches, themselves unbranched; in a cyme the main axis bears perhaps but two branches, these in turn being branched). Pax reinstated, unfortunately, the order of flowering as part of his definitions; the advance of the textbooks has not always been marked by an increased understanding of the facts! The authors of the well-known Bonn textbook of 1894 based their concept on the relative degree of branching of main and lateral axes. In the eighteenth edition, however, of 1930, we find the distinction of Hofmeister and Sachs reinstated—the relative growth of main and lateral axes; this in spite of the obviously greater inherent difficulties in the concept (as pointed out above).

The separation of groups of inflorescences by the relative degree of branching of main and lateral axes had been stated by Wydler, who in 1851 classified inflorescences in three groups instead of the usual two: racemose, cymose, and paniculate. The idea was developed by Čelakovský in 1892, who used the terms "subordinate" verus "coordinate" branching. In the simple raceme, for instance, there are only two "generations" of subordinate branches, the main axis and the lateral shoots or pedicels; the latter, which are numerous, are coordinate. The cyme has many generations of subordinate branches, but in each generation the number of coordinate

[5] Éléments de botanique. Première partie. Organographie. I–XII, 1–276. 1857.

branches is limited, usually to one or two. In the panicle both subordinate and coordinate branches are unlimited. The accompanying diagrams (fig. 6) make clear the fundamental difference between "racemose" or monopodial and dichasial or sympodial branching and illustrate the applicability of Čelakovský's idea.

If this line of thinking be followed further, it will be seen that it largely destroys the distinction between "racemose" and "cymore"; for a simple dichasium has the same form as a raceme with a terminal flower; and, as I have shown elsewhere, it is impracticable to distinguish between simple and compound inflorescences (see also below under raceme, spike, panicle). In fact, as Goebel pointed out, transitions from "racemose" to "cymose" may occur in a single species. The true distinction is evidently not one between modes of flowering but springs from physiological processes as yet not understood: in one type the factors which cause the development of axillary buds are concentrated towards the terminal part of the main axis (and of each successive subordinate axis); in the other type branching may extend back for some distance and be best developed the farther one goes from the apex. Goebel used the terms *akroton* (acrotonic) and *basiton* (basitonic) to express these conditions (fig. 6).

It seems, therefore, that a rational classification of inflorescences must discard the rigid distinctions of the past. It may be based on the simple dichasium as a fundamental type. This is often reduced, by failure of the lateral buds to develop, to a single terminal flower; or, by abortion of one of its flowers, either terminal or lateral, to an apparently forked or one-sided group of two. From it can be derived, by continued acrotonic development, the compound dichasium; and those more specialized monochasial types the cincinnus, the bostryx, the rhipidium, the drepanium, and "false" umbels and capitula (see below). All these may be referred to as sympodial. If many axils of a shoot put forth flowering branches (single flowers or clusters) in basitonic development, and if the subtending leaves of the flowering branches are reduced to bracts, the result is a raceme. From this may be derived the well-known monopodial types, the corymb, the umbel, the capitulum. The terms spike and panicle need special treatment.

Though the frequency of the various types of inflorescence is not strictly germane to their definition, it may be well here to correct the mistaken impression to be gained from several textbooks (FT, RP) that the "cymose" types are much less frequent than the "racemose." This error is doubtless responsible for the current very inadequate treatment of the former. It would be difficult to say which of the two groups actually leads in number of species, but there is probably no great preponderance. The grasses and composites run up the total of monopodial types; aside from these large families, I should guess that the sympodial inflorescences have

the best of it. One has only to mention some of the well-known families and genera which are characterized by dichasia, monochasia, etc. to realize how wrong the textbooks are in their estimate of the importance of such types. Without any attempt at a systematic survey the following come to mind: *Juncus*, *Allium*, *Brodiaea*, Amaryllidaceae, Iridaceae, Commelinaceae, *Anemone*, *Ranunculus* and many other Ranunculaceae, *Helianthemum*, *Drosera*, Portulacaceae, Caryophyllaceae, Crassulaceae, *Philadelphus*, *Saxifraga*, *Rosa*, *Geum*, *Fragaria* and many other Rosaceae, Geraniaceae, *Oxalis*, *Linum*, *Malva*, *Hypericum*, *Cornus*, Melastomataceae, Gentianaceae, Apocynaceae, Asclepiadaceae, Polemoniaceae, Hydrophyllaceae, Boraginaceae, Labiatae, Solanaceae, Rubiaceae, Caprifoliaceae, Valerianaceae, *Campanula*.

Cyme. From the Latin *cyma*, a young sprout of cabbage; this in turn from the Greek κῦμα, something swollen. It has been sometimes used in a more or less classical sense to designate "le sommet d'une plante" (JBB) or simply a "tuft" (WW); also the branches of a tree, taken all together as distinct from the trunk (DC). L used the term for the inflorescence of *Viburnum* and *Cornus*, defining it as consisting of several primary peduncles arising from the same point, as in an umbel, but these bearing secondary peduncles at various points. In this sense he was followed by SFG and JP. But Link in 1798 called attention to the order of flowering; in some of these flat inflorescences the central flower blooms first, between two lateral flowers which open later. And Roeper in 1826 distinguished the cyme as definite or determinate. Thenceforth almost all definitions incorporated in the Linnaean concept some reference to the termination of the growth of the axis and the beginning of blooming in the center (BDJ, AC, R & F, B & B, AR, LHB, MLF, GL, HOP, CD, OED, WD). A representative American definition of today is "a usually broad and flattish determinate inflorescence, i.e., with its central or terminal flowers blooming earliest" (MLF).

DC had an individual concept, which corresponded, curiously enough, to what was later to be known as a group of cincinni: the term cyme "se dit de l'assemblage de deux ou plusieurs pédoncules qui partent d'un même point comme dans l'ombelle, s'étalent à peu près horizontalement, et portent, sur leur face supérieure, une ou plusieurs rangées de fleurs; par exemple, les Sédums." Later (1827) he described under this head a compound dichasium (though this term had not then been introduced). Many followed him in this, speaking more or less clearly of the repetition of branching below each successive terminal flower (JL, GWB, JHB, GB, JCW, CTW). JL floundered in a bog of words: "Suppose the branches of a deliquescent panicle to become short and corymbose, with a centrifugal expansion indicated by the presence of a solitary flower seated in the

axillae of the dichotomous ramifications, and a clear conception is formed of what is called a cyme." The clarity of this conception is perhaps what caused English writers to follow de Candolle rather than their own Lindley. It is interesting to notice that the identification of a cyme with a compound dichasium which was general in the middle of the 19th century has apparently persisted in England but has been abandoned in America. The lack of any clear grasp of the situation by modern American writers may perhaps be attributed to Asa Gray, who in the *Manual*, the *Lessons*, and the *Text-book* offered several confused and more or less contradictory definitions of a cyme. In the *Elements* of 1836 he said, "there are, however, many cases in which the central flowers open first and the lowermost or external ones last. . . ." and goes on to describe the compound dichasium of *Cerastium* and *Stellaria*, in which the "central" flowers *of each branch* flower before the lateral ones, which overtop them (fig. 3); and under the same head he includes the more or less umbelliform cymes of *Sambucus* and *Cornus*, in which flowering is simultaneous, centripetal, or irregular. In the *Text-book* of 1842 we read: "But if the buds of all the upper axils appear in the form of single flowers, a kind of reversed spike or raceme is produced . . . which blossoms from the summit downwards, the terminal flower being the oldest." (No examples of this.) In the first edition of the *Manual* (1848), he reverts to the dichasium, using cyme for either the simple or the compound cluster; but again foists "centrifugal flowering" on the compound dichasium, saying that flowers are "*most likely* to spring from the axils of the upper leaves" (italic mine). In 1864 the term is maintained for this same confused concept. And finally in 1877 we read: "When all the secondary axes connected with the inflorescence are arrested by terminal flowers, without any onward growth except what forms the footstalks or pedicels, and these are nearly equal in length, a raceme-like inflorescence is produced. . . . These are distinguished from the true raceme . . . by the reverse order of development of the blossoms. . . ." The term dichasium had then been in use more than 40 years; but it had apparently remained unrecognized by our leading writer of textbooks. In the statements quoted above we find the ancestors of the statements in our most recent texts. Gray finally discovered or decided to recognize the European treatment of inflorescence and included it in a long footnote in the the sixth edition of his text-book (1879). But he retained the old definitions in the body of the work, including that of the "descending raceme," with its unnamed figure.

From this short history we can see how the three current notions of the cyme became established: the compound dichasium, now found mainly on the other side of the Atlantic Ocean; the Linnaean flat-topped cluster with the idea of centrifugal flowering grafted on; and the extraordinary "upside-down raceme" of the textbooks.

In view of the preceding discussion of "determinate" and "indeterminate," it would seem best to abandon these terms from our classification, as I have already suggested; and with them the wholly misleading idea of "centrifugal" versus "centripetal" flowering. The word cyme may be conveniently restored to its ancient meaning: a compound, more or less flat-topped inflorescence, exemplified by *Sambucus* and *Viburnum*. This is essentially the Linnaean concept but somewhat less rigidly defined, for some of these inflorescences do *not* have their primary branches consistently arising from one point, nor all their secondary branches scattered.

Other types of inflorescence which have been embraced by this term are better referred to terms which may be more precisely defined, as those which follow.

Dichasium. From the Greek δίχασις, a division, referring to the apparent dichotomy of a dichasial system. The term was introduced by Schimper and published by Braun in 1835. In the original discussion it seems to refer to the system of branching rather than to any particular group of flowers; and this vagueness is maintained by subsequent writers. It was never widely adopted by English or American botanists, and is completely lacking from most of the works here cited. Only AC, BDJ, JCW, CTW, SGJ, GL include the term in their glossaries. Since we frequently need a term for the simple three-flowered unit, which is basic to an understanding of inflorescence in general, it would seem best to reserve the term dichasium for this meaning: a peduncle bearing a terminal flower and two bracteoles which subtend lateral flowers. A repetition of this sort of branching from the axils of the bracteoles of the lateral peduncles forms a compound dichasium (figs. 3, 6). Later branches are apt to go over to a monochasial type (see below). It would seem unnecessary to coin special terms for the various complex systems which may ensue; since the plan is fundamentally that of a dichasium the term compound dichasium may embrace them all; unless the transition occurs at the first branching, in which case the inflorescence may be spoken of as paired monochasia (fig. 8). If by immediately repeated dichasial branching several cincinni arise from almost the same point, we get a cyme which flowers centrifugally, as in some species of *Sedum* (fig. 9).

Monochasium. From the Greek μόνος, one, and χάσις, separation, presumably by analogy with dichasium. (The latter, however, is not derived from a word meaning "two" and χάσις, but from δίχα, asunder; but these words are all connected.) The term monochasium was introduced by Eichler in 1875 in his *Blüthendiagramme*.

In 1837 the brothers Louis François and Auguste Bravais published a classic paper on "the symmetrical disposition of inflorescences." As the title suggests, they were concerned chiefly with the orderly succession of

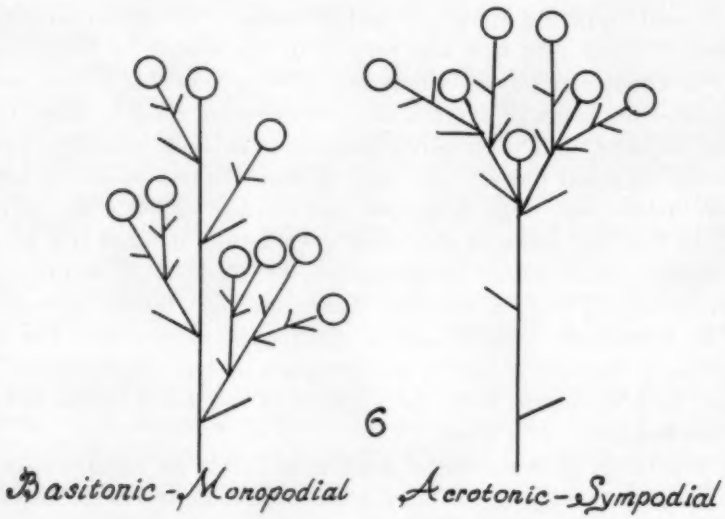
branches; and, in taking up centrifugal flowering ("évolution centrifuge"), they made it clear that this was related to the system of branching and "non à la succession physiologique des développements." They were the first to name the types of sympodial inflorescences, classing them as *cimes unipares, bipares,* and *multipares,* according as each peduncle produced (besides its terminal flower) one, two, or more lateral flowering branches. The *cime bipare* was what Schimper had already called a dichasium; although the Bravais' knew of Schimper's work they ignored this term. The *cime unipare* was renamed monochasium by Eichler. It signifies an inflorescence formed from a terminal flower and one lateral peduncle subtended by a bracteole (which may be abortive or deciduous). The number of branches is limited to one by the presence of but one bracteole on the peduncle, as in monocots, or by the abortion of the flower in the axil of one of the two bracteoles of a dicot.

The repetition of monochasial branching forms an inflorescence which may be termed a compound monochasium. Since, however, the latter takes various forms which have their own special names (see below), the distinction between simple and compound monochasia is unnecessary.

As each lateral branch in turn apparently continues the growth of the peduncle from which it springs (and whose growth is actually terminated by its flower) a sympodial or "false" axis is formed (fig. 7). The form of the monochasium depends on the way in which the single bracteoles, or the fertile bracteoles of each pair, are disposed around the axis. There are four types, discussed below under the terms bostryx, cincinnus, rhipidium, drepanium.

Like dichasium, the term monochasium has been ignored by most American writers, and is poorly represented even in those English works which accord dichasium some space. BDJ has "a uniparous cyme, either pure, or resulting from the reduction of cymes (Urban)"—the meaning of which escapes me. CTW have "a cyme in which the branches are spirally arranged or alternate or one is more strongly developed than the other"—a completely wrong concept. The term is lacking from JCW. Only SGJ has a fairly clear explanation of it. Gray's tardy recognition of the sympodial inflorescence has already been mentioned. His misunderstanding of various monochasia is mentioned below under drepanium. OED's definition is more likely than not to confuse the reader: "Eichler's name for that form of cymose inflorescence in which the main axis produces only a single branch." CD has a completely erroneous definition: "A cyme with one main axis"; and WD's is the same.

Pleiochasium. From the Greek πλείων, more, and χάσις, separation. (See above on the derivation of monochasium.) The term was introduced by Eichler in 1875 in the *Blüthendiagramme* in place of the *cime multipare*



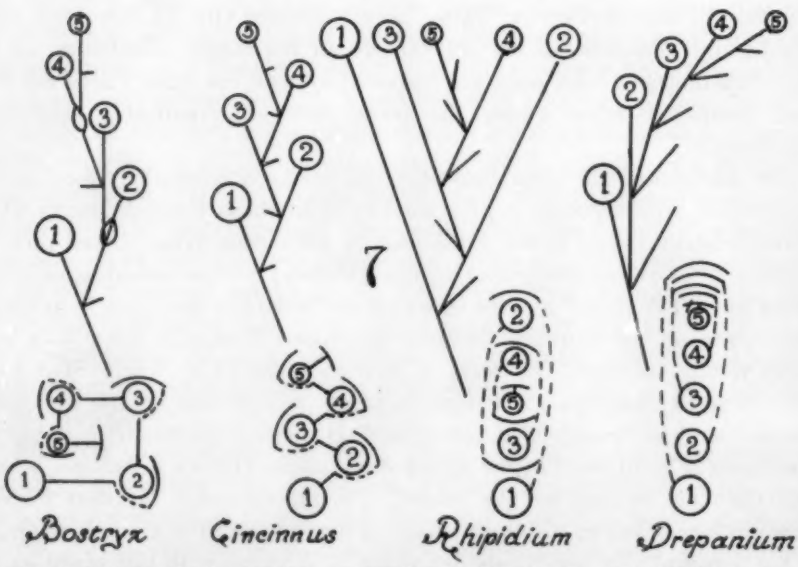


FIG. 6. Diagrams illustrating contrasting tendencies in the development of inflorescences; the circles represent flowers, the short lines bracts and bracteoles. No order of flowering is represented. FIG. 7. Diagrams of monochasia: side view above, plan below. The circles represent flowers, numbered in order of development; the short lines bracteoles. In the plans each flower is connected by a line (solid or broken) with the curved line representing the fertile bracteole on its pedicel; this in turn subtends the next following flower. The spiral twist of the bostryx is indicated by the representation of the bracteoles successively in profile and face view. The cincinnus, if coiled, would turn away from the observer, below the plane of the paper. Rhipidium and drepanium are flattened in the plane of the paper.

of the Bravais'. It refers to a cymose inflorescence in which more than two lateral branches spring from a single peduncle. Of the botanical works here cited only BDJ has a definition. OED and CD have "a cyme with three or more lateral axes," which is scarcely clear; WD has a correct definition, but, curiously, under polychasium, a term which I have seen in no other work (no pleiochasium is to be found there).

Eichler himself wrote: "Die Pleiochasien sind von wenig morphologischen Interesse und von geringer Verbreitung (Arten von *Euphorbia, Sedum, Damasonium* etc.)." After the first pleiochasial branching, the inflorescence usually goes over to a dichasial or monochasial type. The inflorescence shown in figure 9 may be regarded as a pleiochasium.

Bostryx. From the Greek *βόστρυξ*, a curl or lock of hair. It was introduced by Schimper and published by Braun in 1835 to designate the kind of inflorescence formed by repeated monochasial branching in which the fertile bracteoles form a spiral around the sympodial axis. It is the *cime unipare hélicoïde* of the Bravais'. BDJ puts it: "A sympodial branch-system in which the right-hand or left-hand branch is always the most vigorous"; but this is an understatement—only one branch at each node develops. In the bostryx of a dicot the right-hand bracteole subtends a branch on every peduncle in turn, the left-hand remaining abortive; or vice versa. In a monocot there is usually but one bracteole; this lies in a plane which diverges from that of the preceding peduncle always in the same direction. JCW has a more or less unintelligible definition. AG in 1879 apparently applied the expression "helicoid cyme" to a drepanium. In SGJ's illustration also a drepanium receives this name, and GL, whose definition is far from clear, has confused bostryx and cincinnus: his "helicoid cyme" is a cincinnus on pp. 744, 751, a bostryx on pp. 741, 755. The bostryx is unknown to modern American textbooks and manuals (though MLF has for helicoid "coiled like a snail-shell"; the genus of snail not specified). Two of the dictionaries consulted have confused the bostryx with the drepanium (CD: "a raceme-like cyme . . . with all of the branches or pedicels upon one side. It is usually more or less coiled." WD: "a cyme with all the flowers on one side of the rachis, usually causing it to curl."). The third (OED) has simply "an uniparous helicoid cyme." The "helicoid" part of the definition obviously should refer to the spiral disposition of the branches, not to any snail-like coiling of the axis or of the inflorescence as a whole. (For misapplications of the word see further Gray's remarks quoted below under cincinnus; also under drepanium.) The plan of a bostryx is shown in figure 7. It must be recalled that it, like all monochasia, is made up of a succession of branches, each a peduncle and forming a terminal flower, each giving off a new branch from a point below the flower; all together forming a sympodial axis which bears flowers laterally. The points of departure of the

flowers from this axis follow a spiral course around it. Examples are *Hemerocallis, Hypericum.* The bostryx may be contracted so that all the pedicels appear to arise from almost the same point, as in *Allium, Pelargonium;* see below under umbel.

Cincinnus. A Latin word meaning much the same as βόστρυξ, a curl of hair, a ringlet. It is connected with the Greek κίκιννος, which has the same meaning. Some have derived the modern term directly from the Greek, spelling it cicinnus The purist may prefer this form, since other names for monochasia are Greek (it is certainly not "erroneous" as BDJ calls it); but the Latin spelling is the more usual.

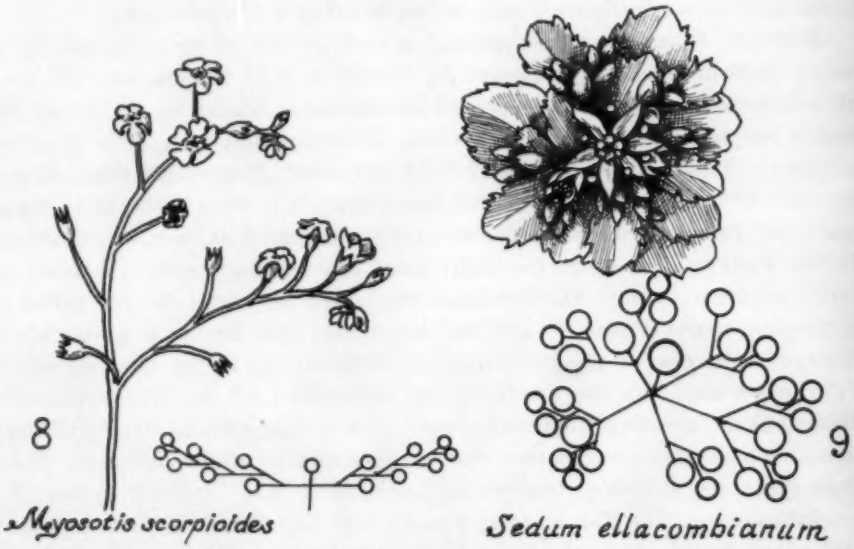


FIG. 8. Paired cincinni of *Myosotis scorpioides,* arising from a dichasium. FIG. 9. Cyme of *Sedum ellacombianum;* after the five main (pleiochasial) branches are formed, a dichasium appears on four of them, the lateral branches of which form cincinni; the fifth passes at once into a cincinnus.

The term was introduced by Schimper but apparently first published by Wydler in 1851. It is the *cime scorpioïde* of the Bravais'. It is a monochasium in which flowers appear alternately to right and left along one side of a sympodial axis. In other words, the points of origin of the flowers follow a zigzag course backwards and forwards on one side of the axis (fig. 7). Perhaps because its growth is thus accentuated on one side, the axis is usually coiled; this is the origin of the "scorpioid" part of the definition. The inflorescence was so characterized by DC in 1827 even before the Bravais' elucidated its relationships to other types. Perhaps for this reason it became known among later writers as a scorpioid cyme more commonly than as a cincinnus. AG in the footnote already mentioned (1879) has this

to say: "Scorpioid and Helicoid have been carefully distinguished by later morphologists, on account of some difference in the mode of evolution and arrangement of the flowers along one side of the rhachis, by which they become two-ranked in scorpioid, one-ranked in helicoid. But practically the two kinds of clusters are not always readily discriminated; and in general terminology a single name, with subordinate qualifying terms, is sufficient. Scorpioid is the older and commoner one, therefore the most proper to be used in the generic sense." This confusion, this failure to grasp essential distinctions, is perhaps a sufficient reason for the subsequent neglect of these terms by American botanists. However, AC, BDJ, GB, JHB, EB, JCW, LHB, GL, OED, WD have more or less clear and accurate explanations either of cincinnus or scorpioid cyme. R & F, MLF have merely "circinately coiled while in bud."

Since the sympodial axis of a monochasium may continue to develop through a long sequence of flowers, and since the youngest flowers are those nearest the apex of this axis, the inflorescence may resemble a raceme. This is particularly true of the cincinnus (which has been called *racemus secundus* and *racemus scorpioides*). The inflorescence of *Claytonia* has been generally described in recent manuals as a raceme; but not only is it secund, the flowers arising alternately to right and left along one side of the axis; but the bracteoles, when present, are clearly *opposite* the pedicels, not below them (the next internode of the axis is axillary, not the flower). The classic example of the cincinnus is of course the family Boraginaceae. *Myosotis*, for example, has in general a compound dichasium of which the branches are cincinni (fig. 8). Curiously, this is recognized in the descriptions of the family by recent writers, but under the genus *Myosotis* the "racemes" are described. Cincinni are conspicuous also in *Phacelia*, *Sedum* (fig. 9), and other genera.

Rhipidium. From the Greek ῥιπίς, a fan, especially for fanning a fire; the Greek diminutive ῥιπίδιον means a small bellows. Buchenau in 1866 introduced the word rhipis; but Eichler in 1875 used the diminutive though less accurate form, which is now in general use.

The number of my authorities who take cognizance of this term shrinks to four and includes no American botanists. BDJ calls it "a fan-shaped cyme, the lateral branches being developed alternately in two opposite directions." JCW is more precise, with "monoch. cyme where each successive branch falls alt. on one side and the other of the relatively main axis, and all fls. are in one plane." Similar definitions are to be found in CD, WD. The inflorescence was explained by Eichler as a bostryx in which each branch was opposite the preceding one; i.e., the angle between successive branches is 180°. This forms a flat, fan-shaped inflorescence in which the bracts are between successive peduncles (fig. 7). (Buchenau had likened it

to a cincinnus; but this would give a different relation between bracts and peduncles; see under drepanium, below.) Examples of rhipidia are found in the Iridaceae; otherwise it seems to be of small importance.

Drepanium. From the Greek *δρέπανον*, a sickle; the diminutive of which is *δρεπάνιον*, a small sickle. Buchenau in 1866 used the former word, transliterating it as drepanum; Eichler in 1875 adopted the diminutive, which form has come into general use (cf. rhipidium).

The inflorescence is defined by BDJ simply and inadequately as "a sickle-shaped cyme." JCW gives the correct meaning; "a monoch. cyme with each successive branch on same side of relatively main axis, and in same plane." Similar definitions are to be found in CD, OED. WD has "a bostryx with the axes in planes parallel to that of the main peduncle." Since the drepanium is not a bostryx, and since a line—or a peduncle—does not define a plane, this definition leaves much to be desired. The drepanium was explained by Eichler as derived from a cincinnus in which all flowers arise in one plane (the median) instead of alternately to right and left. This brings all the successive bracts on the same side of the group of flowers (fig. 7). (Buchenau had erroneously derived his drepanum from a bostryx, which would yield the arrangement of flowers and bracts found in a rhipidium.) Examples are found in Juncaceae, Marantaceae.

A helicoid cyme (bostryx) may be said to have "all the flowers following a descending spiral." This idea has been curiously misapplied to the drepanium by AG (1879), SGJ, CD, WD, GL. See SGJ's explanation of helicoid: "all the flowers in a downward curve to one side of the parent axis"; also Gray's footnote quoted above under cincinnus—perhaps the ancestor of all these perversions.

Raceme. From the Latin *racemus*, a bunch of grapes, or similar fruit. This is one of L's terms, and was defined in 1751 as consisting of a peduncle with short lateral branches. The examples given were *Vitis*, *Ribes*. The illustration is of a pendent raceme; and JBB incorporates this feature into his definition (contrasting the raceme in this respect with the thyrse, which is upright). WW has simply "bunch." DC, SFG, JL, GWB, JP, JHB, AC, R & F, AR also abide by the Linnaean definition; most, however, state or imply that the raceme is a "simple" inflorescence, i.e. that the lateral branches of the main axis are themselves unbranched, one-flowered. AG brings in the idea that the apex of the axis continues to grow and add lateral flowers, and that "the lowest blossoms are of course the oldest and therefore open first" (1864). Thenceforth this concept, expressed often merely by the word indeterminate, creeps into the definitions (EB, B & B[6], BDJ, JCW, LHB, GL, CTW, HAG; and all the textbooks except TST). Almost all recent authors also regard the raceme as "simple" in the above sense.

[6] But they have "determinate"; which I take to be simply a misprint.

For reasons already adduced, it is clear that the definition should be revised; unless we are to coin new terms for the many racemes which have terminal flowers and for those which flower in other than acropetal sequences. Moreover, there is no need for limiting the term to simple clusters. Many species have a variable type of raceme which sometimes but not always produces small clusters instead of single flowers in the lower axils; it is unnecessary to refer these to some other term, when one will suffice for both types of growth. I propose, therefore, to restore something like the original definition, in all its simplicity. A raceme is a monopodial inflorescence composed of a central axis along the sides of which are arranged pedicellate flowers or small flower-clusters, usually arising in the axils of bracts; flowering is commonly but not necessarily acropetal, and the axis may or may not be terminated by a flower.

There are two difficulties with such a definition. (1) There is no sharp line between a raceme and a series of solitary flowers in the axils of ordinary leaves, since there is often a gradation from foliage leaves to bracts (as in *Antirrhinum*). (2) There is no sharp line between a raceme and a panicle or thyrse, since the further branching of the lateral branches may yield one of these. Such difficulties merely illustrate the well-known fact that nature is not so rigid as we like our definitions to be.

As HAG and others have pointed out, it is often difficult to distinguish a bractless raceme from a bractless cincinnus. In fact the cincinnus may also be termed a sympodial raceme; if this is desirable, the definition suggested above may easily be modified to include both monopodial and sympodial types (cf. umbel).

Corymb. From the Greek κόρυμβος through the Latin *corymbus*, a cluster of ivy berries, or of other berries. To L it was a simple inflorescence with the pedicellate flowers on the same level; this was adopted by JBB, WW, SFG, GWB, JP, JHB. DC called it also "fausse ombelle"; in 1827 he changed his definition, applying corymb to compound inflorescences in which "l'axe central suit la loi des inflorescences terminées, et les branches latérales celle des inflorescences indéfinies," giving for examples the Compositae in which the "indefinite" capitula are arranged "cymosely." According to DC, Pliny had used corymbus for globular capitula, and others had used it in many other senses. To GB it was a flat-topped panicle. But in general the Linnaean sense has been preserved into modern times, with the usual addition of the "indeterminate" plan of growth and flowering (AG, EB, AC, BDJ, B & B, JCW, CTW, HAG, WD, OED, CD). R & F, MLF seem undecided with "a flat-topped or convex open flower-cluster; in the stricter use of the word equivalent to a contracted raceme and progressing in its flowering from the margin inward." HAG also admits that it is "sometimes loosely applied to any type of flower-cluster of similar shape"; without saying whether his own usage is thus loose. Several modern

writers surprisingly abandon precision altogether. AR has "a flat-topped or convex flower-cluster with the outer flowers opening first"; with no mention of the "racemose" disposition of the pedicels—the definition applies equally well to an umbel or to the capitulum of Compositate, as well as to some cymes. LHB, GL express themselves in like fashion. Such definitions abandon the really characteristic feature of a corymb, but cling to the outworn concept of order of flowering. Many authors have used the term for the inflorescences of *Crataegus* and other plants which scarcely fit their own definitions in any respect (AG, R & F, MLF, HAG). All the textbooks, however, agree on the corymb as a raceme with the flowers carried up nearly to the same level, and opening centripetally. With the expurgation of the last provision, this definition may well stand; it will apply to various *Rubi*, Cruciferae, etc.

Umbel. From the Latin *umbella*, a little shade, hence a parasol or umbrella; diminutive of *umbra*, shade.

This has always signified an inflorescence having branches arising from the same point (or nearly so) on a common peduncle. To L it was a form of *receptaculum*, to be understood in terms of his concept of the *flos aggregatus*. JBB distinguished between "true" and "false" umbels, the former being those of the Umbelliferae and characterized by the fruit of that family. Others adopted the Linnaean concept but changed the status of the umbel from that of a receptacle to that of an inflorescence (WW, DC, SFG, JL, GWB, JP, AG 1848, JHB, GB, AC, OED, CD). AG in 1864 added that the umbel is centripetal; to subsequent writers it was indeterminate (EB, BDJ, B & B[7], LHB, GL, WD; and all the textbooks). However, a number of recent botanists omit any reference to the order of flowering, which in view of the examples which some of them use, is just as well (R & F, JCW, AR, CTW, MLF). HAG calls it racemose; which, considering his explanation of the latter term ("all flowers axillary and lateral, the axis therefore theoretically capable of indefinite prolongation") does not seem particularly applicable.

Umbels are usually exemplified by the Umbelliferae and Primulaceae; but a number of authors name *Asclepias*, *Pelargonium*, and/or *Allium* as examples (AG 1864, TST, WIS, RP, HOP, RW, N, WD). Practically all modern systematists treat these plants and their relatives as umbellate. To the extent that they define umbels merely by their form (branching from one point) this is justified. Unfortunately some, particularly the writers of textbooks, clearly class the umbel as "centripetal" even when they adduce as examples the sympodial clusters of *Asclepias*, *Allium*, *Pelargonium*. N, defining the umbel as centripetal, illustrates it by a photograph of *Pelargonium* which shows clearly the unopened buds pendent around the open flowers.

[7] Again we find "determinate," surely a misprint for "indeterminate."

To avoid coining a new term for these clusters, it would seem best to retain the term umbel in a wide sense (as defined, for instance, by MLF), but to distinguish (if only for purposes of classification) between the strictly monopodial umbels of Umbelliferae and Primulaceae and the sympodial umbels of Liliaceae, Amaryllidaceae, Geraniaceae, Asclepiadaceae, etc. In at least one of these it has been shown not only by superficial examination but by morphological study[8] that the inflorescence is composed of contracted bostryches or cincinni (as the monopodial umbel is really a contracted raceme).

Spike. From the Latin *spica*, a point, an ear of wheat. Although this etymological meaning refers to a compound inflorescence, and although L was thinking of the grasses when he formulated his definition (see his figure), he defined a spike as a group of sessile flowers arranged alternately upon a simple common peduncle. He probably considered the spikelet a "flos aggregatus"; but the lack of morphological clarity has persisted to our own time. The Linnaean definition was adopted by all later authors, but mostly without regard to the alternate disposition of the flowers or branches. JBB applied the term also to "fleurs pédunculées & disposées en long aux extrémités des tiges." Indefinite flowering comes in with DC in 1827 but is little emphasized in later definitions. Many, however, repeat L's original error, that the spike is "simple" (SFG, JL, GWB, AG, JHB, GB, EB, BDJ, R & F, JCW, CTW, AR, MLF, LHB). This is unfortunate, since to follow this definition (which none of these authors do) would mean the exclusion of many if not most of the inflorescences to which the term is commonly applied. The spike of grasses is obviously compound, since the main axis bears spikelets, not sessile flowers. Many of the "spikes" and "interrupted spikes" of Labiatae are composed of closely aggregated and contracted dichasial or monochasial clusters; and the same is probably true of many Scrophulariaceae, such as *Verbascum thapsus*, often given as an example of the spike. While histological studies are scarce, it is probable that many aments and spadices are derived from compound inflorescences and so "simple" only in a gross sense.

The situation is easily clarified by defining the spike simply as composed of an elongated axis bearing sessile or almost sessile flowers singly or in contracted clusters.

Spadix. From the Greek σπάδιξ, itself connected with the verb σπάω, to tear off, etc.; and so meaning a bough or branch torn off, especially a palm frond. The Latin *spadix* had the same significance (among several other meanings). Spathe is from the Greek σπάθη, Latin *spatha*, which referred to various broad flat instruments and so to the sheathing petiole of a palm leaf or to the sheath around the base of the inflorescence. It was natural,

[8] Weber, Erna. Entwicklungsgeschichtliche Untersuchungen über die Gattung *Allium*. Bot. Arch. **25**: 1–44. 1929.

then, for L to define spadix as "receptaculum palmae enatum intra spatham, in ramulos fructificantes." His immediate successors omitted the reference to the palm. WW has merely "a sheathed fruit-stalk," and SFG "a supporter accompanied with a spathe." To DC in 1827 it was any sheathed inflorescence of monocots, simple or branched. Very early the term was specifically applied to the other conspicuously spathe-forming group, the Araceae. JBB even defined it exclusively as the "réceptacle que l'on observe dans les fleurs des arum." As a result of this the spadix came to be defined as a *fleshy* spike enclosed in a spathe (JL, GWB—who includes the pistillate inflorescence of *Zea mays*,—AG, EB, AC, BDJ, B & B, LHB, GL, WD, OED), or "a fleshy spike characteristic of the aroid family" (FT). Finally, the pendulum reaches the end of its arc with such definitions as those of R & F, BDJ, AR, MLF: "a spike with a fleshy axis" (cf. also JHB, GWB, B & B, HAG, CD). AG said a spadix is "merely" a fleshy spike, "usually" enveloped in a spathe.

The word spadix, in brief, from meaning a sheathed inflorescence, as of a palm, has come by gradual steps to refer to a thickened, fleshy spike, with or without a sheath, as in Araceae. The latter meaning is now so firmly established in the literature as to make a return to the earlier sense most undesirable.

Capitulum, Head. Diminutive of the Latin *caput*, head. L used it to designate a cluster of several flowers compacted into a globular mass, and in this sense it has been widely adopted, generally with the provision that the flowers are sessile or nearly so (WW, DC, SFG, JL, GWB, AG, GB, B & B, R & F, JCW, AR, HAG, LHB, GL, MLF, TST). In the early days what we now know as the head of Compositae was distinguished by other names; but AG includes thistle and dandelion in his examples though his definition speaks of a "round or roundish" cluster, and the more modern writers would also use the term for Compositae though their definitions do not always embrace a flattened disc. Several authors go as far as to define the head or capitulum as the inflorescence of Compositae (JHB, FT) or to give only Compositae as examples (HOP). BDJ has "the capitulum of Compositae" for a definition of head, capitulum being defined as "a close head of sessile flowers." GL likewise vacillates, in the opposite direction, his capitulum being the inflorescence of Compositae, while the head has the more inclusive definition as "a compact inflorescence." GB is similarly vague with "a compact globular or roundish cluster"; and AC says "also [applied] to other more or less compact inflorescences, as the spike, corymb, and panicle." GB also thinks of a head as "strictly speaking . . . a globular spike or a globular panicle of which the branches are excessively short." The head is thought of as a spike also by AR, LHB, WIS, WD; while AG and others liken it to an umbel.

The indeterminate plan of flowering is added to the concept by EB, WD, CD, and implied by many others (JL, AG, GB, WIS, HOP, FT). This introduces the same difficulties as those encountered with the umbel. While many heads, as those of *Trifolium*, are indeed monopodial, other clusters so named are sympodial; e.g. those of *Cornus, Cephalanthus*. Long ago WW used for examples species of *Mentha* and *Thymus:* highly complex in their inflorescences. If these are to be included, the indeterminate feature must be omitted from the definition, and we may then recognize both monopodial and sympodial capitula. For the same reason, any stated or implied reference to the "simplicity" of the capitulum must be avoided; a sympodial head is necessarily "compound."

Ament, Catkin. *Amentum* originally signified a thong fastened to a weapon; how it came to acquire its botanical application is not clear. L described as "amentaceus" an aggregate flower with a filiform scaly receptacle. To JBB the *chaton* was "une espèce de réceptacle commun à un grand nombre de petites fleurs incomplètes, ordinairement unisexuelles," which might apply to many things besides catkins as we know them. WW has "a composition of flowers and chaff, on a long, slender, thread-shaped receptacle." DC defined it as "assemblage de fleurs sessiles, ou presque sessiles, sur un axe central, qui, au lieu d'être permanent comme dans l'épi, tombe de lui-même. . . ." SFG has yet another idea: "the flowers borne upon bracteae which are themselves borne upon an axis." JL specified the complete lack of perianth and the deciduous habit, without mentioning shape. GWB's definition unites all these features. JP dodges, with "inflorescence of the Amentaceae"; and AG has little more than "the peculiar scaly spike of Birch, etc. . . ." GB's definition is similar. JHB calls it a "deciduous unisexual spike." And so it goes: various authors use the spicate, elongate form, the unisexual flowers, the lack of perianth, the scaly bracts, the deciduous habit in all possible combinations of two or more. And of course the "indeterminate" order of flowering comes in also, though with few observations to substantiate it. To all authorities here quoted an ament is a spike (to some a "spike-like raceme"); to JCW, HOP, TST, OED it is pendulous or often so; to LHB, GL "usually flexuous." To all but JCW, FT, OED it is scaly-bracted (to HAG also "dense"). Only BDJ, LHB, AR, MLF, and the dictionaries specify that the flowers are unisexual; and only B & B, R & F, HAG, and the dictionaries mention that they are naked or apetalous. Only BDJ, GL, CD, and WD have them deciduous as a whole.

So this familiar term, the meaning of which I suppose every systematic botanist, every teacher of elementary botany thinks he knows, can be assigned no exact sense by consulting modern glossaries and texts. The only way to a sound definition is through better observation of the inflorescences

to which we wish to apply the term. All are long and slender, many are pendulous. All have unisexual flowers (save teratological specimens). The aments of *Quercus* and *Castanea* are not bracteate, at least when they are mature, nor are their flowers destitute of perianth; but all such inflorescences lack petals. So far, only the unisexual flowers distinguish aments from other spikes, such as those of Polygonaceae, to which the term is never applied. Apparently the most reliable character to define them is that aments are deciduous as a whole. So, if we wish to preserve current *usage* (as distinct from current *definitions*, which are too various), we may define the ament as a slender, often pendent spike bearing unisexual, apetalous flowers, and finally deciduous as a whole.

Panicle. From the Latin *Panicula*, the gossamer or down of plants, a catkin; a diminutive of *panus*, a swelling, an ear of millet. Its application to inflorescences is not obvious. To L it was a sparse inflorescence variously divided; much the same as the modern meaning. But it has had an involved career.

JBB, WW, SFG repeated L. DC introduced the concept that the basic plan of a panicle is a raceme, which has been followed by most writers since then; many have defined the term, indeed, simply as a "compound raceme," meaning, presumably, a raceme which bears lateral racemes in place of single flowers (EB, B & B, AR, LHB, JCW, GL, OED: and, less definitely, HAG, CTW). To AC the lateral branches are "either determinate or indeterminate"; and in this he is followed more or less explicitly by SGJ, HOP, FT, WD. On another line of thought, JL mentioned the "deliquescent" panicle, in which the "rachis itself separates into irregular branches, so that it ceases to exist as an axis." And to JP, GB, R & F, BDJ, MLF, CD, TST, and apparently sometimes HAG and CTW the panicle is any loosely branched inflorescence, no basic plan or order of flowering being mentioned. JHB defined it as the "inflorescence of grasses," and WIS have apparently the same idea today. The elevation of the term by Wydler and Čelakovský to designate a class of inflorescences distinct from "racemose" and "cymose" has already been discussed.

In this variously branched and loosely arranged cluster of ideas one can discern no precise pattern to serve as a model for future usage. In searching for a meaning one may well first inquire into the nature of the objects to which the term is to be applied. It is clear that the inflorescence of oats is racemose; but the panicle of *Panicum* perhaps is not, since the spikelet of the Panicoideae has a different organization. The inflorescence of *Yucca* (when it is compound) and of certain other Liliaceae seems to be indeed a compound raceme. The word is also used of Compositae (e.g. *Aster*), referring to the arrangement of the capitula, which are not racemes but which do flower centripetally. But the "panicles" of *Clematis virgini-*

ana are composed of dichasial elements; so are those of *Thalictrum*, of *Hydrangea paniculata*, of *Vitis rupestris*, of *Scrophularia;* and of course the "panicled cymes" of various Saxifragaceae and Valerianaceae. (It is significant also that the thyrse—which see—is regarded by many as a type of panicle; it is commonly formed of dichasia: *Penstemon, Syringa, Vitis.*) To cease referring to all these clusters as panicles would be to impose an useless restriction on our vocabulary; particularly since the expression "compound raceme" is concise and self-explanatory and need not monopolize the term panicle. It is expedient to restore something like the original meaning of the latter term: a loosely branched inflorescence of which the ultimate units may be of various types.

Thyrse. The θύρσος in classical Greece was a wand wreathed with ivy and vine, carried by the devotees of Dionysios; more generally the word meant any wand or shaft, especially the stalk of an umbelliferous plant. L used it for a "coarctate panicle of ovate form"; a coarctate panicle being one with the pedicels appressed, or at least not divaricate. JBB distinguished the thyrse as being an erect sort of raceme, his raceme proper being always pendent. To WW a thyrse was merely a "cluster." DC, followed as usual by JL, defined it as a compound raceme whose lower branches are shorter than those in the middle. SFG had it a very compact panicle, an oval head; and GWB had much the same idea. Many defined it even more vaguely, as simply a compact panicle, sometimes referring to it as ovoid or cylindrical or conical (JP, AG, EB, AC, R & F, B & B, JDW, AR, MLF, GL).

In 1827 DC defined the thyrse as a mixed inflorescence, composed of small cymes along an axis of indefinite growth, as in Labiatae, *Lythrum*, etc. This was partly a protest against characterizing such groups as verticils, which, he said, are rare in nature. He distinguished spiciform and racemiform thyrses. In most respects his concept was not followed by others, but limitation of the term to mixed inflorescences was accepted by JHB, BDJ, LHB, GL (as "more correctly . . . ."), HAG (sometimes), WD, OED, CD.

In general the inflorescences called by this name may be characterized as mixed in the above sense. In view, however, of the definition of panicle proposed above, and of the close connection between panicle and thyrse, it would seem best to define the latter more loosely, in the words of many of the older botanists: a compact panicle of more or less cylindrical form.

SUMMARY

1. This discussion has shown that the terms used for inflorescences are often so defined as to be inapplicable to the types of flower-clusters for which they are intended; some, indeed, have very rare, if any, counterparts

in nature. Moreover the classification of inflorescences into "indeterminate" (centripetal or acropetal) and "determinate" (centrifugal or basipetal) groups refers to their behavior rather than to their structure and is not conducive to clear understanding of the modes of flowering. The terms "monopodial" and "sympodial" more accurately describe the results of contrasting methods of development of inflorescences; for the underlying difference adoption of the terms "basitonic" and "acrotonic" is suggested.

2. In order to fit the terms we use to the parts for which we use them, revised definitions are proposed as follows:

Cyme: a compound, more or less flat-topped sympodial inflorescence, sometimes simulating a compound umbel but the branches less regularly disposed.

Dichasium: a typically three-flowered cluster composed of a peduncle which bears a terminal flower and, below it, two bracteoles which subtend lateral flowers. (The bracteoles may be abortive; and one or two flowers also may fail to develop.) A compound dichasium arises from repetitive branching of a simple dichasium.

Monochasium: a sympodial inflorescence composed of a peduncle which bears a terminal flower and, below it, a single fertile bracteole which subtends a lateral flower; the peduncle of the latter in turn giving rise to a single lateral branch; and so on. (The bracteoles may be abortive.)

Pleiochasium: like a dichasium, but the peduncle giving rise to three or more lateral branches.

Bostryx: a monochasium in which successive pedicels describe a spiral around the sympodial axis.

Cincinnus: a monochasium in which successive pedicels follow a zigzag path along one side of the sympodial axis.

Rhipidium: a bostryx compressed so that all flowers lie in one plane.

Drepanium: a cincinnus compressed so that all flowers lie in one plane.

Raceme: a monopodial inflorescence composed of a central axis along the sides of which arise pedicellate flowers or small flower-clusters, usually in the axils of bracts.

Corymb: a raceme whose pedicels are proportionally elongated so as to bring all the flowers more or less to the same level.

Umbel: an inflorescence (monopodial or sympodial) composed of several branches which radiate from almost the same point and which are terminated by single flowers or by secondary umbels.

Spike: an inflorescence composed of sessile or almost sessile flowers arranged singly or in contracted clusters along a central axis.

Spadix: a spike with a thickened, fleshy axis and usually enveloped by a spathe.

Capitulum (Head): a compact inflorescence (monopodial or sympodial) comparable to a spike with a very short (often discoid) axis, or to a contracted compound dichasium.

Ament (Catkin): a slender, often pendent, usually scaly spike bearing unisexual, apetalous flowers, and finally deciduous as a whole.

Panicle: a loosely branched inflorescence of which the ultimate units may be of various types.

Thyrse: a compact panicle of more or less cylindrical form.

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ADDITIONAL SPECIES OF SYNCHYTRIUM WITH PROSORI[1,2]

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In a previous publication the author (1955c) reported the occurrence of prosori in the so-called summer cycle of eight species of *Synchytrium* in which they had been overlooked. Inasmuch as the presence of a prosorus is recognized as a subgeneric distinction, this discovery necessitated a reclassification of these species, and they were placed provisionally in the subgenus *Microsynchytrium*. Since that time other species have been restudied cytologically, and a prosorus has been found to occur in their summer cycles also. The present paper concerns its presence in such species as well as a description of the morophological characteristics and the outstanding reactions which such species induce in their hosts. It is based in part on a study of living and fixed material collected by the author, a restudy of the late Dr. M. T. Cook's prepared slides and herbarium specimens which he generously gave to the author, and on herbarium material and prepared slides from other sources.

Synchytrium Geranii. This species was described by Clendenin (1895) on *Geranium carolinianum* in Louisiana and later reported from the same locality by Cook (1945a, 1945c). Bartholomew (1927) reported it on the same host in Kansas, and the author has collected it in Texas, Louisiana, Mississippi and Florida. Clendenin and Cook described the galls, sori, sporangia and resting spores, but Cook's measurements of the galls and sporangia are incorrect. Both of these workers overlooked the presence of a prosorus in the life cycle of this species. In living material as well as in fixed and stained sections the author found that the initial cell functions as a prosorus, and this has been confirmed from a study of Cook's preparations. The empty and collapsed prosorus is also evident at the right of Cook's (1945c) photograph 6B. When empty it lies above the sorus of sporangia, and in this respect *S. geranii* is similar to *S. stellariae*, *S. cerastii*, *S. boerhaaviae*, *S. perforatum*, *S. epilobii*, and *S. tillaeae*. This is illustrated in figure 1 which also shows a small connecting plug of densely stained material between the soral and prosoral walls. This plug may be comparatively small and inconspicuous, oval to almost circular, 4–6 μ, in cross section (fig. 2), or fairly large (fig. 3). As the author (1955b) pointed out the presence of this structure in a sporangial gall is an effective key to recognition of the occurrence of a prosorus in the life cycle of *Synchytrium*, even when the prosorus is empty, collapsed and hardly recognizable as such. Compared

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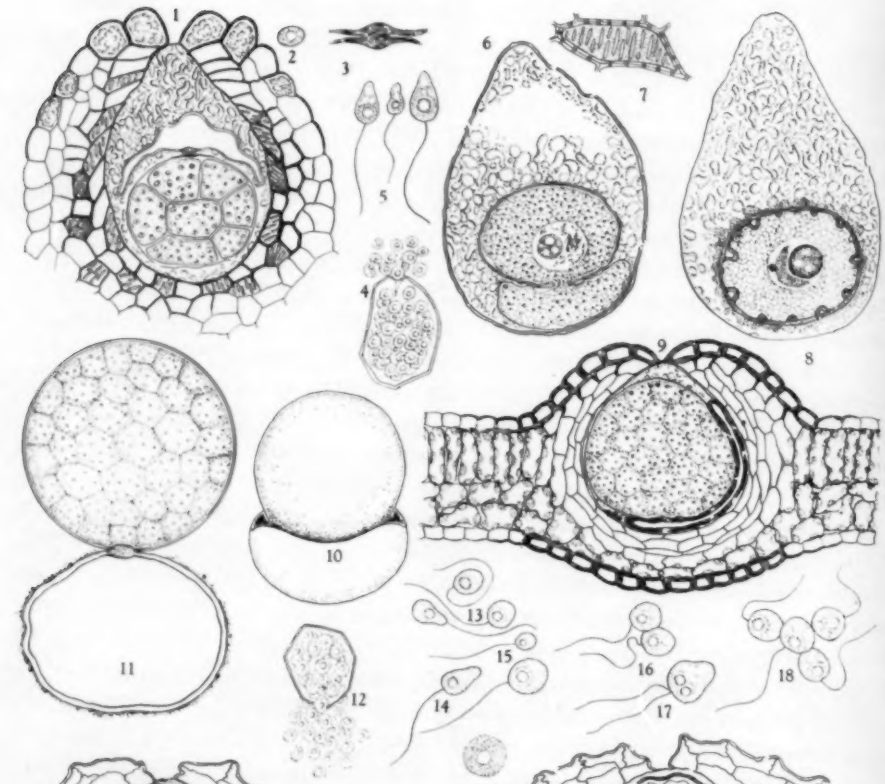
with the infected cell, the mature prosorus is usually small, 50–138 μ in greatest diameter, subspherical, or oval in shape, with a 2–2.8 μ thick wall, and lies in the base of the host cell with a large amount of residue above it.

The sorus begins as a small vesicle on the lower surface of the prosorus, and as more protoplasm grows or flows out it may become flattened against the base of the infected cell and somewhat reniform in shape (fig. 6.). With further growth and expansion, however, it apparently pushes the prosorus upward so that the two structures eventually occupy the relative positions shown in figure 1. In living material they may be dissected out fairly readily, and the empty prosorus comes out as a partially collapsed vesicle attached to the sorus in the region of the plug. The residue in the infected cell is usually so abundant that the empty and collapsed prosorus is often obscured in fixed and sectioned material and this is probably the reason why it has been overlooked in this species. The mature sorus is subspherical, oval, or ellipsoidal in shape, 50–150 μ in greatest diameter, with a fairly thin hyaline wall which shows a faint cellulose reaction when tested with chloro-iodide of zinc. Cook reported that the maximum size of the sporangia is 7.5 μ, but apparently this is a miscalculation. In the living condition they are predominantly polyhedral, 27–60 μ, in greatest diameter. The zoospores of this species have never been reported, but the author has found them frequently in early March and April. They are oval to elongate, 3–3.2 $\times$ 4–4.2 μ, in shape with a tapering anterior end, a small, light-orange refractive globule, and a 12–15 μ long whip-lash flagellum (fig. 5). The exceptionally small and large zoospores vary from 1.8–2 $\times$ 3 μ to 4 $\times$ 6.5 μ respectively, and numerous large ones with two globules and flagella are fairly common. Paired zoospore may occur, but no unmistakable stages of fusion have been found. The resting spores of *S. geranii* may be solitary or up to 4 in a cell, and in the latter instances they may be angular in outline from mutual contact and pressure. They are quite large, predominantly subspherical, up to 210 μ in diameter, to oval and ellipsoidal, 130–160 $\times$ 150–220 μ, in shape. In many fixed and stained sections the inner surface of the incipient spore wall was papillate or verrucose as shown in figure 8. The low broad papillate or warts were numerous or sparse at this stage, but in mature resting spores they were lacking.

Synchytrium geranii is one of the most conspicuous species of the genus because of the large tumors it may induce on the stem, petioles and leaves of its host. These may be 5–250 mm in diameter and are brilliantly red in color from the anthocyanin present in the sheath and neighboring cells of the aggregated and confluent galls. This species induces the development of both sporangial and resting spore galls which are composite and multicellular and strikingly similar in size and shape. Accordingly, it is a compositely dihomeogallic species in relation to its host (Karling 1955d). Although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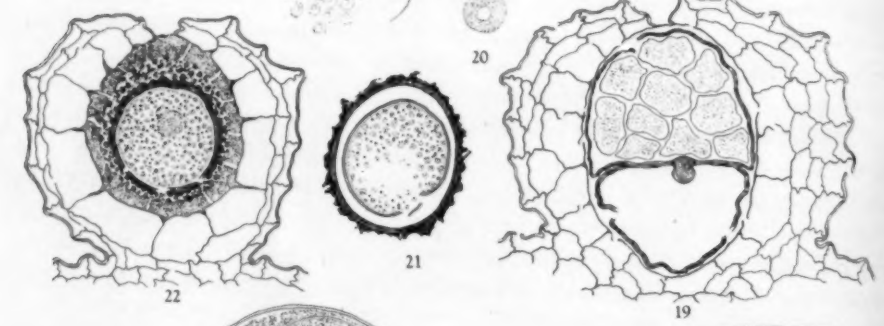
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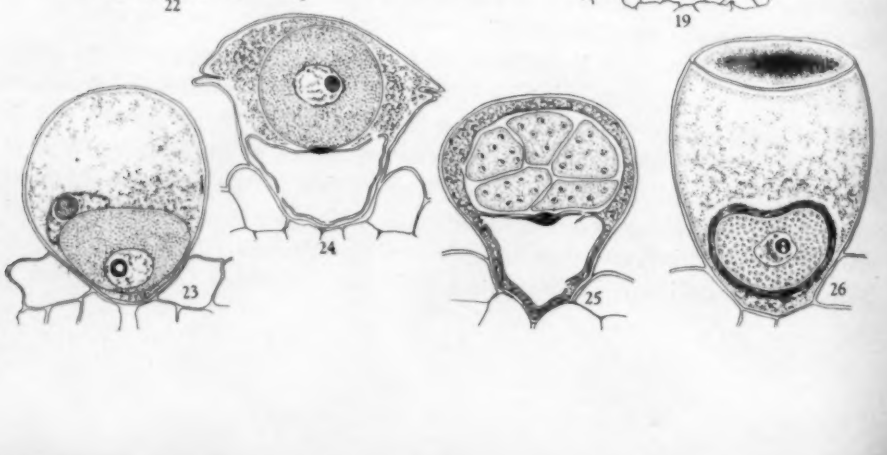
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their successive developmental stages have not been fully observed, present evidence suggests that the galls are formed by a marked enlargement of the infected cell and division or multiplication of the adjacent epidermal, palisade and mesophyll cells. No division of the infected cell has been seen, and the healthy adjacent cells are not very greatly enlarged except at the apex (fig. 1) of the galls as is shown by Clendenin's figure 3. The single and isolated galls usually protrude conspicuously on the surface of the host, and the protruding portion is somewhat dome-shaped or almost hemispherical and crateriform. The lower portion of the gall is usually embedded in the host tissue to the extent that the opposite lower side of the leaf may protrude also. The shape of the sporangial and resting spore galls *in toto* is somewhat broadly pyriform, 250–500 μ broad by 320–650 μ high with a sheath which may be 4–6 cells in thickness. The aggregated and compressed galls in the large tumours tend to be elongately polyhedral. In herbarium material which has been thoroughly soaked in water, they may be readily separated by dissection and frequently have the superficial appearance of minute grains of wheat.

In addition to stimulating enlargement and division of its host cells, *S. geranii* also causes thickening, lignification and differentiation of the walls of the sheath cells, particularly in the resting spore galls. This may involve the epidermal cells at the apex as well as those of the sheath to a distance of 3–6 cells as shown in figure 1. Such sheath cells may have numerous scalariform perforations (figs. 1 and 7) like tracheary elements. As a result of this thickening and lignification of the walls the mature galls are hard and woody in texture and very difficult to section and dissect.

Another reaction to infection is an increase in and modification of the

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FIGS. 1–8. *Synchytrium geranii*. FIGS. 9–18, *S. edgertonii*. FIGS. 19–22, *S. marginale*. FIGS. 23–26, *S. amsinckae*. FIG. 1. Small gall with empty prosorus and sorus of sporangia; wall of sheath cells thickened and differentiated. × 133. FIGS. 2 and 3. Plug in cross and longitudinal section. × 333. FIG. 4. Sporangium discharging zoospores. × 300. FIG. 5. Variations in uniflagellate zoospores. × 1000. FIG. 6. Infected cell showing formation of sorus. × 182. FIG. 7. Lignified and differentiated sheath cell. × 300. FIG. 8. Infected cell with resting spore whose inner wall is verrucose. × 200. FIG. 9. Sporangial gall with empty prosorus and sorus of sporangia; upper and lower epidermal cell walls thickened. × 133. FIG. 10. Living sorus sitting in empty basal prosorus. × 133. FIG. 11. Living sorus of sporangia and attached prosorus. × 200. FIG. 12. Sporangium discharging zoospores. × 400. FIG. 13. Zoospores shortly after discharge. × 1000. FIG. 14. Zoospore in swimming phase. × 1000. FIG. 15. Variations in size of uniflagellate zoospores. × 1000. FIG. 16. Paired zoospores. × 1000. FIG. 17. Large biflagellate zoospore. × 1000. FIG. 18. Cluster of zoospores. × 1000. FIG. 19. Sporangial gall with sorus and empty prosorus. × 160. FIG. 20. Plug in cross section. × 333. FIG. 21. Resting spore with plasmolysed, hyaline endospore and content. × 360. FIG. 22. Resting-spore gall with layers of residue around spore. × 160. FIG. 23. Sporangial gall with prosorus and enlarged host nucleus. × 225. FIG 24. Partially collapsed sporangial gall with incipient sorus and empty, basal prosorus. × 225. FIG. 25. Sporangial gall with sorus, sporangia, and empty prosorus. × 225. FIG. 26. Large resting spore gall with spore. × 225.

cytoplasm of the infected cell. This becomes evident very shortly after infection, and as the host cell enlarges the cytoplasm becomes foamy in appearance. Later, as the prosorus, sorus and resting spore mature the remainder of the infected cell becomes partly or wholly filled with globules and bodies (figs. 1, 6 and 8). In living dissected galls the residue comes out as amber to light-brown globules, 2–12 μ in diameter. They may be single, or adhere in compact groups as polyhedrons. In fixed, sectioned and stained galls the bodies may be oblong, elongate and connected to form a loose reticulum, as shown in Clendenin's figure 3. They occur equally as abundantly in the sporangial as in the resting spore galls (figs. 1 and 8). The host cell nucleus enlarges markedly in size and may reach a diameter of 35μ and persist until the sorus and resting spores are mature. However, it has not been found to become lobed and irregular in shape.

Several attempts were made to infect *Geranium pusillum* and *G. maculatum* with zoospores of *S. geranii* under favorable greenhouse conditions at Purdue, but they were unsuccessful, which suggests that this parasite may be limited to *G. carolinianum*.

Synchytrium Edgertonii. This species was collected by Cook (1945a) on *Dichondra repens* in Louisiana He reported the presence of sporangial galls, sori, and sporangia but apparently did not observe prosori, resting spores, and resting spore galls. However, in material collected in Louisiana, Texas and Florida the author found that *S. edgertonii* is a long cycled species which develops prosori, sori, sporangia, zoospores and resting spores, and the occurrence of prosori has been confirmed by the discovery of their presence in Cook's slides. The mature prosorus is subspherical, 135–204 μ, or oval, 140–160 $\times$ 156–192 μ, with a light-amber to yellowish-brown, 3–4.8 μ thick, wall and yellowish content. As its content flows out to form the sorus and the latter expands against it, the prosorus becomes invaginated. In fixed and stained sections it frequently lies at one side of the sorus, as is shown in figure 9 and Cook's (1945c) photograph 7 D. The empty collapsed prosorus and sorus may be dissected out of living galls quite readily. Frequently, the two come out together and look like a globule (the sorus) sitting in a shallow bowl (the invaginated prosorus) as shown in figure 10. By further dissection and stretching the prosorus can be pulled out into its globular shape again, so that it and the sorus have the appearance shown in figure 11.

The sorus is oval to oblong, 135–140 $\times$ 220–328 μ, and spherical, 180–278 μ, in shape with a 2.5–3 μ thick, hyaline wall and amber-yellow content. The sporangia are numerous, up to 250 in a sorus, polyhedral in shape, small, 18–32 μ in greatest diameter, with a thin hyaline wall and dark-yellow to light-orange, granular content. Zoosporogenesis, dehiscence of the sporangia (fig. 12), and the initial behavior of the zoospore are fundamentally similar to those of most species of *Synchytrium* and need not be described further. Immediately after emerging the zoospores are almost spherical, 3.2–4 μ, to

broadly oval in shape (fig. 13), but during the actively motile stage they are more elongate and almost oblong with a tapering anterior end (fig. 14). Each zoospore contains an almost spherical, 1.2–1.6 μ nearly hyaline to light-amber or yellowish refringent globule and has a 11–14 μ long whiplash flagellum. Some of the uniflagellate zoospores are minute. 2 μ, or quite large and 5.6 μ in diameter (fig. 15).

Numerous biflagellate and biguttulate zoospores (fig. 17) were observed, and these looked like they might be zygotes resulting from a fusion of gametes. For this reason special attention was given to the possibility that gametic fusion might occur in *S. edgertonii*. Numerous paired quiescent zoospores were seen (fig. 16), which after a brief period of rest swam away together. Although such pairs were studied for long periods of time, actual fusion was not observed. Also, zoospores in groups of 3 to 6 were occasionally found (fig. 18) which suggested that the central one might be a female gamete surrounded by male gametes as reported by Kusano (1930) and Köhler (1932) for *S. fulgens* and *S. endobioticum*, respectively. However, such groups dispersed or the zoospores degenerated without fusion occurring. Although no fusions have been observed it is possible that the motile cells of this species might be facultative gametes which require special conditions for fusion.

The resting spores of *S. edgertonii* are usually solitary but occasionally 2 to 3 may occur in the infected cell. They are oval to spherical in shape. 120–192 μ in diameter, yellowish to light-brown in color with a smooth, 3–4.2 μ thick, light brown wall and coarsely granular content. They may be enveloped by a sparse or fairly large amount of residue.

The sporangial and resting spore galls induced by this species are basically similar in being composite and multicellular so that this species also may be described as being compositely dihomeogallic. They may occur singly or scattered on the host, or are aggregated and confluent. In the latter instances the infected portion of the leaf, stem or petiole may be 3 to 4 times its normal diameter. Also, in the region of isolated galls the leaf may be more than twice its usual thickness as is shown in Cook's (1945c) figures 7B and 7E. Both types of galls are usually embedded in the host tissue and as such do not protrude very conspicuously. They are predominantly oval to narrowly and broadly pyriform, 198–328 μ high by 240–288 μ broad, with a sheath 3 to 6 cells in thickness (fig. 9). The inner sheath cells adjacent to the infected one are compressed or flattened and elongate. The walls of the epidermal cells above and below the gall usually become greatly thickened and lignified, and this thickening may also extend inward to the lateral walls of cells immediately underneath. Laterally, it extends over a circular to oval or irregular area of the epidermis, so that most of the gall lies between these plaques of thickened epidermal cells as shown in figure 9.

The upper and lower plaques of thick-walled and lignified epidermal

cells make it very difficult to section the galls well. They also seem to play a role in the release of the fungus from the host. As Cook (1945c) pointed out and showed so well in photographs (1945a), the fungus may drop out and leave a hole in the leaf at the site of the galls, and he attributed this to general breakdown of the host tissues. The author has found that the thin-walled epidermal cells bordering these plaques, and the sheath cells underneath may break down at maturity somewhat like an abscission layer. The plaques of thick-walled epidermal cells then drop off or out, leaving the infected cell and a few sheath cells exposed above and below so that they readily fall out.

Synchytrium marginale. This species was collected by H. S. Jennings on *Trifolium carolinianum* in Texas, April 2, 1890. According to Cash (1954), Ellis apparently identified and named this species for Jennings, but neither of these workers published a description of it as far as the author is aware. Herbarium specimens were secured from the U. S. Department of Agriculture through the courtesy of Dr John A. Stevenson and accompanying this material is a descriptive note of *S. marginale* which presumably was written by either Jennings or Ellis "Galls clustered in tuberculiform masses. Mostly marginal, greenish, becoming brown, formed by the enlargement of several contiguous (epidermal)? cells, each cell containing 3 or more globular resting spores, 100–150 μ diameter with a thick rugose epispore."

Fixed and stained sections were made of Jennings' material, and although badly shrunken they, nevertheless, showed that *S. marginale* is a long-cycled species which develops prosori, sporangia and resting spores. In this material the galls occur abundantly along the veins and margin of the leaves where they form conspicuous, elongate elevations, cushions, or thickenings which may project 300–500 μ above the surface of the host. The galls are usually aggregated and confluent, and only a few single and isolated galls were found in the material studied. The sporangial and resting spore galls are basically similar in being composite and multicellular as shown in figures 19 and 22. When single and isolated both types of galls usually protrude conspicuously above the surface of the host and are largely superficial. When aggregated and confluent they are more deeply buried in the host tissue. The sheath appears to be from 3 to 5 cells in thickness, but its cells are so shrunken that very little can be said about their relative sizes. However, the cells immediately adjacent to the infected one are greatly enlarged.

Although no migration stages of the protoplasm to form a sorus were found in Jennings' material, the occurrence of a prosorus in the summer cycle of *S. marginale* is clearly evident. In most sections of the sporangial galls examined a collapsed empty vesicle was present in the base of the in-

fected cell. In a few sections the vesicle was not collapsed so that the infected cell appeared to be bilocular with a cavity in the base and a sorus of sporangia in the upper part as shown in figure 19. In such sections the infected cell had the same appearance as those shown by the author (1955a, 1955b) for *S. ranunculi* and *S. cellulare*. Also, the thickened area or plug between the sorus and prosorus wall was present in all sections. It varies from 12 to 18 μ in diameter (fig. 20)with a hole, 4–6 μ in diameter in the center. In figure 19 it projects down into the empty prosorus. The presence of this plug is additional evidence of the occurrence of a prosorus in this species.

Inasmuch as *S. marginale* has never been described in the literature the following diagnosis is made on the basis of present information.

Prosorus subspherical, 90–110 μ, or oval with a 2.5–3.5 μ thick wall, lying in base of infected cell when empty and collapsed. Sorus subspherical, 95–142 μ, oval, 102–120 × 130–140 μ, or almost hemispherical, with a 2.8–3.2 μ thick wall. Sporangia numerous, predominantly polyhedral, 28–48 μ in greatest diameter, with a thin hyaline wall and finely granular content. Zoospores unknown. Resting spores usually solitary, subspherical, 91–120 μ, oval, 90–98 × 108–120 μ, with a smooth 3–4.2 μ thick exospore, a 1.8–2.3 μ thick hyaline endospore, and coarsely granular content; enveloped by a thick layer of residue which may fill remainder of infected cell; germination unknown.

Compositely dihomeogallic, galls usually aggregated and confluent along the veins and margins of leaves, single and isolated galls protruding and largely superficial. Sporangial galls 228–240 μ high by 248–254 μ broad; resting spore galls 240–252 μ high by 216–246 μ broad, sheath several cells in thickness.

On leaves and petioles of *Trifolium carolinianum*, College Station, Texas, U. S. A.

It is to be noted in this diagnosis that the resting spores are smaller than reported in the note mentioned above. This may be due partly to shrinkage since 1890 when the material was collected. Also, the spore wall appears to be smooth instead of rugose. The hyaline endospore is usually withdrawn from the exospore and stands out quite clearly. In most sections of the dried herbarium material the residue around the spore seemed to be made up of two layers, a crumbly one adjacent to the spore and an outer dense, more homogeneous layer (fig. 22). The latter was cracked by somewhat radial lines so that under low magnification it appeared to be composed of more or less rectangular cells. Obviously, many of the appearances, structures and dimensions noted above have been modified by shrinkage, and the description of them will doubtless have to be changed somewhat when living material is studied.

Whether or not *S. marginale* is a valid species remains to be seen. So far 24 species of *Synchytrium* have been reported on members of the Leguminosiae, and two, *S. aureum*, and *S. trifolii*, on species of *Trifolium*. *Syn-*

chytrium aureum, on *T. pratense*, *T. humile*, *T. minus* and *T. repens*, is a short-cycled species and differs thusly from *S. marginale*, but it is possible that investigators may have mistaken the resting spores of *S. aureum* for those of *S. marginale* and overlooked the sporangial stages. *Synchytrium trifolii* which has been reported on *T. pratense* is invalid, according to Magnus (1902), and relates to *Physoderma* (*Urophlyctis*) *trifolii*.

Synchytrium Amsinckiae. This species was collected, described and named by McMurphy (1913) on *Amsinckiae intermedia* in California. It is a simply dihomeogallic species in relation to its hosts in that it causes only simple, unicellular sporangial and resting spore galls. McMurphy described and figured the initial cells as being transformed directly into a sorus of sporangia at maturity but in fixed and stained sections which were prepared by Dr. D. A. Johansen of the California Botanical Materials Co., the author found that the initial cell functions as a prosorus and gives rise to a sorus. Accordingly, *S. amsinckiae* is the first of the simply dihomeogallic species in which a prosorus has been found to occur in the so-called summer cycle.

The prosorus usually lies in the base of the enlarged epidermal cell and is oval, 42–48 × 52–72 μ, subspherical 45–76 μ or almost hemispherical in shape with a large nucleus (fig. 23) which may be up to 28 μ in diameter. No migration stages of the protoplasm to form the sorus were observed, but numerous cases of empty prosori in the base of the cell with sori lying above them were found. Figure 24 shows a partially collapsed gall with a uninucleate incipient sorus in the apex and an empty prosorus in the base of the infected cell, and figure 25 shows a mature sorus with sporangia. In both of these figures the plug of densely stained material between the sorus and prosorus is present. However, compared with other species it is quite small in *S. amsinckiae* and may be only 5–10 μ in diameter. Although no migration stages were observed, the presence of this plug and an empty, partially collapsed vesicle in the base of the infected cell are clear-cut evidence, in the author's opinion, that *S. amsinckiae* develops a prosorus in its summer cycle.

The reaction of the host to infection is limited largely to a single cell so far as it is known. The infected cell enlarges rapidly, protrudes conspicuously on the surface of the host, and eventually becomes predominantly obpyriform, 150–265 μ high by 100–200 μ broad at the apex, in shape with a reddish-brown wall. The host nucleus enlarges conspicuously as the infected cell increases in size so that by the time the prosorus is mature it may be somewhat lunate in shape and up to 15 × 35 μ in diameter with a large densely stained nucleole. The latter is not fragmented, nor is the nucleus deeply lobed or irregular in shape as in cases of infection by *S. anomalum*, *S. anemones*, *S. perforatum*, and other species. It usually lies above and in close contact with the prosorus, as shown in figure 23. Infection

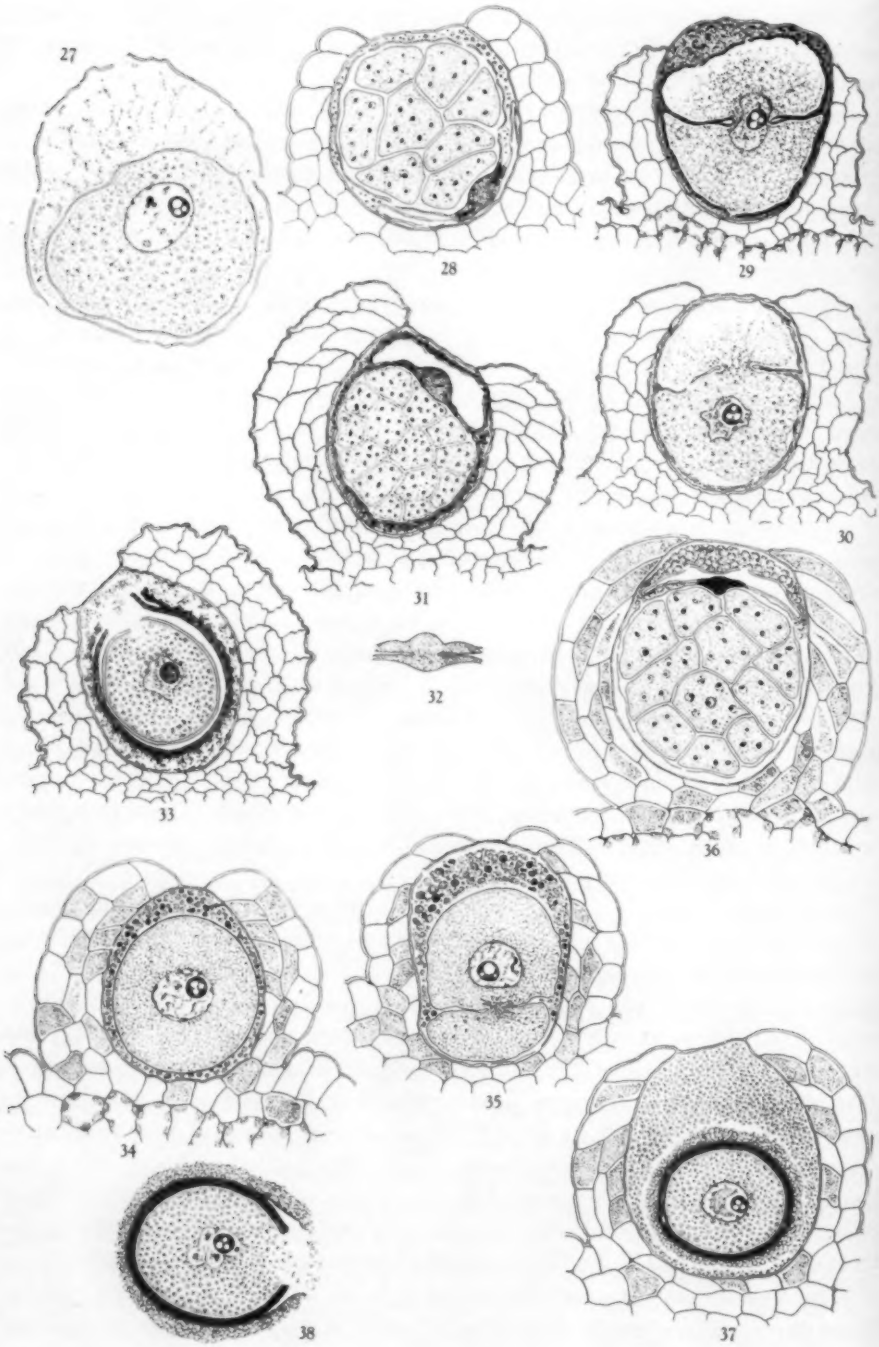
also causes a marked increase in the amount of cytoplasm, and this becomes apparent later as a layer of reddish-brown residue around the sorus, prosorus (fig. 23) and resting spore (fig. 26).

The tapering base of the gall usually extends down to the palisade and mesophyll cells, and those immediately beneath the gall may become greatly enlarged and almost isodiametric in shape. Occasionally, the epidermal cells around the base of the gall enlarge outward (fig. 24) but not to the extent that they form a protruding sheath around the base. So far no division of the epidermal cells has been found.

Synchytrium Impatientis. This species was collected and described by Cook (1951) on stems, petioles, and leaves of *Impatiens pallida* and *I. biflora* in Louisiana. He reported only the occurrence of sori and sporangia, and his description suggests that the initial cell functions directly as a sorus. However, in studying his prepared slides and herbarium specimens, the author found that *S. impatientis* is a long-cycled species which develops prosori, sori, sporangia and resting spores. That the initial cell functions as a prosorus is suggested by Cook's figure 6 which shows a collapsed vesicle in the base of the infected cell, and this has been confirmed from a study of his slides. The prosorus is spherical, 110–180 μ, to ovoid, 98–120 $\times$ 135–170 μ, in shape with a large, up to 30–48 μ, primary nucleus, fills $\frac{1}{3}$ to $\frac{1}{2}$ of the host cell and is surrounded usually by foamy host protoplasm (fig. 27). Stages in the development of the sorus from the prosorus have not been found, but in galls with mature sporangia a collapsed vesicle is present in the base of the cell (fig. 28). Also, present is the characteristic thickened plug of material between the sorus and empty prosorus, which may be up to 26 μ in diameter and 12 μ thick in the center. These structures in the base of the host cell are evidence, in the author's opinion, that the initial cell functions as a prosorus.

The mature sorus is subspherical, 130–200 μ, or ovoid, 115–140 $\times$160–190 μ, and may fill the greater part of the infected cell (fig. 28). The sporangia are predominantly polyhedral, 25–48 μ in greatest diameter with a thin hyaline wall. The resting spores are spherical, 152–195 μ, ovoid, 162–178 $\times$ 189–200 μ, with a 5–7 μ thick, smooth, dark amber wall and coarsely granular content. That Cook saw but misinterpreted the resting spores is evident from his photographs. His figures 3–5, for instance, show resting spores instead of sori. The wall of these spores may be enveloped by a dense, compact layer of residue, as shown in Cook's figures 3–5, but sometimes this layer may be lacking. In most galls the remainder of the infected cell is filled with a crumbly and scattered mass of residue which is usually in the form of connected globules. This is well illustrated in Cook's figure 3.

This species causes a marked reaction in its hosts. The infected cell enlarges to the extent that it may be as much as 400 μ in diameter and is sur-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rounded by a sheath which may be 2–10 cells thick. Accordingly, the sporangial and resting spore galls are composite in structure and vary markedly in size and shape. The majority of galls are somewhat dome-shaped and usually narrowly crateriform at the apex. On the stem such resting spore galls may be 480 μ high by 1044 μ broad, while the sporangial and resting spore galls on the leaves vary from 144 to 280 μ high by 264–300 μ broad. In exceptional cases the galls may be very small as is shown in Cook's figure 2. Also, a few galls have been found which were completely embedded in the leaf tissue and caused no protrusion on the surface of the leaf. The epidermal cells around the protruding portions of the large galls are not enlarged, but they appear to have undergone numerous vertical divisions to keep pace with the enlargement of the gall. In the small galls, however, they are considerably enlarged (fig 28). The inner sheath cells in the lower portion of the galls on the stem are unusually enlarged and may reach a diameter of 100 μ Those in the apex are less enlarged but considerably larger than normal cells It is thus obvious that *Synchytrium impatientis* causes unusual enlargement of the infected cell and division and enlargement of the adjacent healthy cells.

Synchytrium Epilobii sp. nov. This species was collected by Drs. Goheen, Wearne and Servoss, July 1, 1949, on *Epilobium francisianum* at North Beach, Harbor Co., Washington, and herbarium material of it was kindly loaned to the author by Dr C. G. Shaw. Inasmuch as it occurs on a species of the family Onagraceae, is long-cycled and develops a prosorus in its summer cycle, it was first believed to be *Synchytrium brownii*, but a study of fixed and stained sections showed that it differs from this species in several respects. Therefore, it is regarded as a new species and diagnosed as follows:

Prosoris subsphaericis, 78–126 μ diam., ovalibus, 72–85 $\times$ 90–108 μ diam., parietibus 1.8–2.4 μ crasso; soris subsphaericis, 80–198 μ diam., ovalibus, 95–132 $\times$ 140–174 μ diam., parietibus 1.2–2.2 μ crasso; sporangiis numerosis, 30–95, polyhedris, 24–50 μ diam.; sporis perdurantibus subsphaericis, 90–114 μ diam., ovalibus, 84–96 $\times$ 102–38 μ diam., endospore hyalinis, 1.2–2 μ crasso, exospore laevis, brunneo, 2–3 μ crasso; germinatione ignoto.

FIGS. 27 and 28. *S. impatientis.* Figs. 28–33, *S. epilobii.* FIGS. 33–38, *S. tillaceae.* FIG. 27. Large, slightly shrunken prosorus surrounded by foamy cytoplasm $\times$ 150. FIG. 28. Small sporangial gall with sorus of sporangia and empty, collapsed basal prosorus with plug. $\times$ 150. FIGS. 29 and 30. Symmetrical sporangial galls showing formation of incipient sorus from apical prosorus. $\times$ 210. FIG. 31. Asymmetrical sporangial gall with sorus, empty prosorus, and plug in apex of infected cell. $\times$ 210. FIG. 32. Plug in longitudinal section. $\times$ 400. FIG. 33. Asymmetrical resting spore gall with resting spore and enveloping residue; hyaline endospore and content contracted. $\times$ 210. FIG. 34. Small sporangial gall with prosorus surrounded by globular residue. $\times$ 150. FIG. 35. Early stage in sorus development from apical prosorus. $\times$ 150. FIG. 36. Large gall with sorus of sporangia and empty, collapsed apical prosorus embedded in residue. $\times$ 150. FIG. 37. Resting spore gall and spore enveloped by a dense layer of residue; remainder of infected cell filled with dense residue. $\times$ 150. FIG. 38. Cracked resting spore showing smooth wall and enveloping layer of residue. $\times$ 150.

Prosorus usually solitary, occasionally 2 in a cell; subspherical, 78–126 μ, ovoid, 72–85 × 90–108 μ, with a 1.8–2.4 μ thick wall; lying usually in apex of infected cell when empty. Sori subspherical, 80–198 μ or ovoid, 95–132 × 140–174 μ, with a 1.2–2.2 μ thick wall, often enveloped by a layer of residue; plug between empty prosorus and sorus unusually large, 12–16 μ thick in center by 25–42 μ in diam. Sporangia numerous, 30–95 per sorus, predominantly polyhedral, 24–50 μ, exceptional ones up to 72 μ in diam., with finely granular content and a thin hyaline wall. Zoospores unknown. Resting spores usually solitary, ovoid 84–96 × 102–138 μ, subspherical, 90–114 μ, with a hyaline, 1.2–2 μ thick, endospore, a 2–3 μ thick, smooth brownish exospore, and coarsely granular content; enveloped by a sparse or fairly thick layer of crusty residue; germination unknown.

Compositely dihomeogallic, galls single and scattered or aggregated and confluent, brilliantly lavender-red, usually protruding conspicuously on surface of host and broadly crateriform at apex; frequently asymmetrical with opening to infected cell slightly subapical. Sporangial and resting spore galls almost hemispherical to subspherical, 120–300 μ high by 144–432 μ broad with a sheath 3–6 cells thick.

On leaves, petioles and stems of *Epilobium francisianum*, North Beach, Harbor Co., Washington, causing stunting of young leaves and curling and distortion of larger leaves when infection is abundant.

The prosori and sporangia of *S. epilobii* (figs. 29 and 31) are similar in size and shape to those of *S. brownii*, but its sori and resting spores may be considerably larger. Also, the number of sporangia per sorus is much greater in *S. epilobii*. The empty prosorus usually lies in the apex of the infected cell or above the sorus (fig. 31) whereas in *S. brownii* it usually lies underneath the sorus. How significant this characteristic may prove to be taxonomically is not certain yet, but in most species studied by the author the relative positions of the prosorus and sorus are fairly constant and specific. The plug of material which develops between the empty prosorus and sorus of sporangia (fig. 31)is much larger and more conspicuous than in *S. brownii*. Furthermore, the size, shape and appearance of the galls induced on the host are different. *Synchytrium brownii* induces galls which are embedded largely in the host tissue, whereas those caused by *S. epilobii* are largely superficial (figs 29 and 30) and frequently asymmetrical (figs. 31 and 33) like those of *S. australe*. The opening to the infected cell is usually very broad (fig. 29–31), and in exceptional cases as much as a fourth of the infected cell may be exposed (fig. 29). After dehiscing, the sporangial galls are distinctly cupulate in appearance.

The origin of the galls is not known, and it is not certain that the infected cell divides as in the case of infection by *S. australe*. So far as is possible to determine from herbarium material the thick sheath appears to have arisen by division of the epidermal and palisade or mesophyll cells.

It is quite evident that the initial cell of *S. epilobii* functions as a prosorus. Numerous stages of migration of the cytoplasm and nucleus from the

prosorus have been found. Figure 29 shows the primary nucleus passing into the sorus, and figure 3 shows a later stage in which the migration of the protoplasm is almost complete. Later, the broad aperture between the sorus and prosorus is filled with a dark staining material which becomes the so-called plug. Its material usually spreads out laterally along the prosorus and sorus walls so that the plug becomes unusually large in diameter (fig. 31 and 32). As the protoplasm of the sorus cleaves into sporangia, and as the sorus expands and pushes against it the prosorus collapses (fig. 31).

So far only two species have been reported on *Epilobium; Synchytrium fulgens* on *E. adenocaulon* and *S. aureum* on *E. adnatum, E. davuricum, E. hirsutum, E. montanum, E. palustre and E. roseum.* According to Kusano's (1930) figures, *S. fulgens* does not develop a prosorus in its summer cycle, and *S. aureum* is a short-cycled species which develops only resting spores. Should *S. fulgens* be found to develop a prosorus as suggested by the author (1954), *S. epilobii* may possibly be identical to it. On the other hand, the *S. fulgens* reported on *Epilobium adenocaulon* may prove to be identical to *S. epilobii.*

Synchytrium Tillaeae sp. nov. This species was collected on *Tillea erecta* by Dr. L. C. Wheeler, April 4, 1945, on the Refetto Hills near Monterey Park, Los Angeles, Co., Calif., and stained sections of it were prepared for the author by D. A. Johansen. It is a long-cycled species which develops prosori, sori, sporangia and resting spores. Because of its large sori and other characteristics as well as large size of the galls it induces on its hosts it is regarded as a new species and is diagnosed as follows:

Prosoris sphaericis vel subsphaericis, 90–120 μ; soris sphaericis, 120–160 μ, vel ovalibus, 125–132 $\times$ 150–180 μ; sporangis numerosis, polyhedris, 30–50 μ; sporis perdurantibus sphaericis, 80–102 μ, ovalibus, 84–98 $\times$ 108–132 μ, parietibus 3–4.8 μ crasso; germinatione ignoto.

Prosori usually solitary, subspherical to spherical, 80–120 μ, with a 1.8–2.2 μ thick wall; lying in apex of cell and embedded in a layer of residue when empty. Sorus subspherical to spherical, 120–160 μ, oval, 125–132 $\times$ 150–180 μ, with a very thin hyaline wall; plug between empty prosorus and sorus, 16–22 μ diameter by 6–8 μ thick in center, usually extending down into sorus. Sporangia numerous, 30–120 per sorus; predominantly polyhedral, 30–50 μ, exceptional ones up to 84 μ in greatest diameter, with a thin hyaline wall and finely granular content. Zoospores unknown. Resting spores usually solitary, occasionally up to 4 in a cell, spherical, 80–102 μ, ovoid, 84–98 $\times$ 108–132 μ, with a smooth, 3–4.8 μ thick wall and coarsely granular content; enveloped by a closely applied, 8–12 μ thick, rough layer of residue; germination unknown.

Compositely dihomeogallic, sporangial and resting spore galls single and scattered but usually aggregated and frequently confluent, usually protruding conspicuously with a slightly constricted base, and broadly crateriform apex, 252–300 μ high by 264–350 μ broad; small galls 120–140 μ high by 150–170 μ broad; sheath 2–4 cells thick.

On leaves, petioles and stems of *Tillaea erecta*, Los Angeles Co., Calif., U. S. A.

That *S. tillaeae* is a long-cycled species whose initial cell functions as a prosorus is evident in figure 35. The full-grown prosorus fills only a part of the infected cell and is usually surrounded by a layer of crumbly residue which is usually composed of globules or irregular bodies (figs. 34 and 35). As in *S. geranii* and other species the sorus is formed on the lower surface of the prosorus (fig. 35), and as it increases in size the prosorus and residue are pushed into the upper part of the infected cell. As a result the major part of the infected cell is free of residue by the time the sorus is mature, and this appearance is characteristic of all sporangial galls observed by the author. The residue is composed largely of globules, and these may be separate or adhere to one another in large groups. Their appearance and size are very much like those described for *S. geranii*. Sometimes the residue in the resting spore galls may be very abundant and fill the remainder of the cells as a continuous mass (fig. 37), and in other cases it may form a coarse reticulum.

As the prosorus collapses in the apex of the infected cell, it is surrounded, except on the side towards the sorus by the dense and deeply stained residue as noted above and is hardly recognizable as a vesicle (fig. 36). However, the plug of material that fills the former opening in the wall is quite conspicuous, deeply stained, and usually projects into the sorus (fig. 36). In the latter respect, *S. tillaeae* differs from *S. epilobii* (fig. 31). Before and after cleavage the sorus expands considerably in size and except for the apex may fill the large infected cell (fig. 36).

The resting spores are enveloped by a closely applied, up to 12 μ thick, layer of residue which makes the spores look as if they have a very thick rough wall (fig. 37). However, by applying pressure to the spores the residue may be cracked off, leaving a distinctly smooth, 3–4.8 μ thick wall (fig. 38).

This species induces a marked reaction in its host which results in development of large, protruding composite sporangial and resting spore galls. The larger part of the gall consists of the greatly enlarged infected cell which may be oval to subspherical in shape and up to 300 μ in diameter. It is enveloped except at the apex by a 2–4 cell thick, sheath of healthy cells which are elongate, somewhat diamond-shaped and slightly curved (fig. 36). They are considerably larger than the neighboring epidermal, palisade and mesophyll cells, and many of them are filled with a more or less homogeneous substance which stains deeply in prepared slides and gives the galls a very dark chromatic color. No infection or early developmental stage of the galls has been found, and the origin of the sheath is not known.

As the infected cell enlarges its nucleus increases markedly in size and

persists for a long time. It usually lies above the prosorus and resting spore, and may be present until the latter have reached maturity. Apparently, infection also stimulates an increase in host cytoplasm and included substances, which are later transformed into the residue described above.

This is the first species of *Synchytrium* to be reported on a member of the family Crassulaceae, but it is quite probable that additional species will be found on such hosts. Recently, the author received a packet of herbarium material of another species on *Sedum douglasii* of the same family which was collected by Drs. J. A. Calder and D. B. O. Saville 5½ miles southwest of Rossland, British Columbia at an altitude of 4000 ft. This species induces single and scattered, or aggregated and confluent, composite galls on both surfaces of the leaf, and causes crinkling, distortion, and sometimes stunting of the leaves. However, only resting spores are present in this material and the species does not appear to be identical to *S. tillaeae*. The resting spores are generally larger, spherical, 120–170 μ, ovoid, 125–132 $\times$ 140–150 μ, with an almost hyaline to light-amber wall and bright yellow content.

On the basis of the occurrence of a prosorus in the so-called summer cycle of the species described above, they are placed provisionally in the subgenus *Microsynchytrium*, pending discovery of the method by which their resting spores germinate. Previously, *S. geranii*, *S. edgertonii*, *S. impatientis* and *S. amsinckiae* seemed to be members of *Eusynchytrium*, but because of the presence of a prosorus they no longer belong here.

The occurrence of a prosorus in the summer cycle seems to be a specific and constant characteristic as far as present observations go. However, the possibility that its occurrence may vary must not be excluded. In view of the variability in life cycle exhibited by chytrids, it is not improbable that the prosorus of a member of *Microsynchytrium* and *Mesochytrium* may occasionally fail to give rise to a sorus and instead undergo cleavage directly into sporangia, and in such cases the prosorus would be indistinguishable from a sorus.

The discovery of a prosorus in the species described above emphasizes again the necessity of developmental and cytological studies for proper identification and classification of *Synchytrium* species.

SUMMARY

1. The initial cell of seven additional species of *Synchytrium*, *S. geranii*, *S. edgertonii*, *S. marginale*, *S. amsinckiae*, *S. impatientis*, *S. epilobii* sp. nov. and *S. tillaeae* sp. nov., has been found to function as a prosorus and give rise to a sorus of sporangia.

2. This discovery necessitates their removal from the subgenus *Eusynchytrium* where they were previously believed to belong, and they are provi-

sionally placed in *Microsynchytrium*, pending discovery of the method by which their resting spores germinate.

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FLOOD PLAIN FORESTS OF THE RARITAN RIVER

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The forests of the flood plain of the Raritan River in New Jersey have been reduced to a few scattered fragments. Most of the flood plain has been cultivated or pastured and is either still so used or is reverting to natural vegetation. Two of the oldest, longest undisturbed, and largest stands of bottomland forest occur along the middle reaches of the river. One is near the town of Raritan a short distance below the confluence of the North Branch and the South Branch of the Raritan River. The other is adjacent to the Somerset airport southwest of Pluckemin and one mile downstream from Burnt Mills which is at the confluence of the Lamington River and the North Branch of the Raritan River. These two forest fragments are suggestive of the magnificent forests that once occurred along this river. Wistendahl (1955) has described the present condition of the rest of the Raritan River flood plain.

The objective of the present study is to record the composition of these forest remnants as indicative of the potentialities of the Raritan flood plain. One can see in these stands what would develop over most of the flood plain with an indefinite period free of man's interference.

The flood plain forest at Raritan occupies a site adjacent to the river. It lies between the river and a poorly drained area typical of the inner side of flood plains. The site is separated from the inner flood plain by a deep slough through which a portion of the river flows at high water, but which is only partially occupied by water during drier seasons. Among local botanists, the site is known as Mertensia "island" because of its islandlike character and the great profusion of *Mertensia virginica* that covers the ground in spring. This site will be referred to as Mertensia "island" in the text of this paper.

The bottom land forests of the river some five miles upriver adjacent to the Somerset airport and near Burnt Mills are more diversified than those at the Raritan location. Three distinctly different stands were studied in detail. One was a small but very fine stand situated topographically very similar to the Mertensia "island" site being only partially separated from the inner flood plain by a deep, water-filled slough. This site will be referred to in the text as the outer flood plain. A second stand lies beyond the deep slough on the inner flood plain, whose surface is undulating, the lower places being shallow, water-filled sloughs in spring and fall, and ice-filled much of the winter. The higher places of the undulating surface support

trees, the trees overhanging and shading the shallow sloughs. A third stand adjacent to the inner flood plain but farther from the river occupies an old river terrace. The terrace lies slightly above the inner flood plain and is apparently rarely flooded. It will be referred to as the river terrace. The three stands were all somewhere near the same size which is approximately 10 acres, the outer flood plain somewhat less, the terrace and inner flood plain stands somewhat more.

Methods. The methods used were the same for all study areas. The sampling of trees that were one inch d.b.h. (diameter at breast height) and over was done on twenty quadrats 10 meters square dispersed at regular intervals along two parallel belts through the stand. Tree cover was measured along four 100 meter transects using the line intercept method as employed by Buell and Cantlon (1950). Sampling of saplings of tree species, those between one foot in height and 1 inch d.b.h., was done on twenty 2×10 meter quadrats nested within the larger quadrats. The numbers of saplings of each species occurring within these was recorded. Also cover contributed by saplings was measured along the transect lines used in obtaining tree cover. At the same time shrub cover was also measured. In both cases the line intercept method was used as developed by Bauer (1943) for study of shrubby vegetation.

Tree seedlings, those individuals less than 1 foot high, were sampled by counts made on 40 $\frac{1}{2} \times 2$ meter quadrats, two of which were located in each of the 10 meter square quadrats.

Nomenclature follows that of Gray's manual, eighth edition (Fernald 1950).

Results. The data obtained by sampling the four stands are presented in three tables: table 1 summarizes transect data for the terrace and the adjacent inner flood plain, table 2 summarizes quadrat data for the outer flood plain and Mertensia "island", and table 3 summarizes the transect data for shrub and sapling cover measurements. All four sites showed certain common features of vegetation but the data do show differences from one site to another that appear obviously to be related to habitat differences.

The total ligneous flora of all four stands, based on the sampling data, consisted of 34 species of which 19 were tree species. The largest number of tree species—14—occurred on the outer flood plain, the smallest number—9—on Mertensia "island", and intermediate numbers—11 and 12—on the terrace and inner flood plain respectively. Eight species of shrubs and 4 species of lianas were recorded in the sampling, with the largest number occurring on the flood plain sites and the smallest number on the terrace (table 3). There were three tree species with individuals which were not over 1″ d.b.h. They contribute as saplings to cover in the shrub layer (table 3). American hornbeam (*Carpinus caroliniana*) is the principal among them

TABLE 1. *Data for tree species of stands located on the terrace and the inner flood plain. D = density or number of individuals per 1000 square meters; F = frequency or the number of times a species occurred in the quadrats expressed in per cent; BA = basal area per 1000 square meters. C = per cent of cover based on line transect measurements. In order to express density in terms of 1000 sq. M. the seedling count was multiplied by 50 and the sapling count by 5.*

	Less than 1" d.b.h.				More than 1" d.b.h.											
	Less than 1' tall		More than 1' tall		1.0–3.9"			4.0–9.9"			10.0" or more			Total BA	C
	D	F	D	F	D	F	BA	D	F	BA	D	F	BA		
Terrace															
Fraxinus americana	—	—	3	5	—	—	—	4	20	1.48	6	40	6.18	7.66	25
Ulmus americana	1150	48	255	30	—	—	—	2	25	0.60	—	—	—	0.60	2
Carya cordiformis	150	15	15	20	—	—	—	1	5	0.19	1	10	0.83	1.02	8
Acer negundo	375	30	25	35	—	—	—	—	—	—	—	—	—	—	—
Tilia americana	50	5	3	5	1	10	0.05	5	30	1.14	1	5	0.28	1.47	3
Acer saccharum	8050	75	685	85	22	80	0.89	16	80	2.95	2	15	1.61	5.45	85
Ulmus rubra	—	—	—	—	1	5	0.01	—	—	—	1	10	0.80	0.81	2
Quercus rubra	25	3	8	15	—	—	—	1	5	0.17	5	35	4.94	5.11	32
Juglans nigra	—	—	3	5	—	—	—	—	—	—	—	—	—	—	—
Quercus velutina	—	—	—	—	—	—	—	—	—	—	2	10	1.33	1.33	5
Carya ovata	—	—	—	—	—	—	—	1	5	0.15	—	—	—	0.15	1
Total							.95			6.68			15.97	23.60	
Inner Flood Plain															
Fraxinus americana	75	5	23	20	—	—	—	3	20	0.92	5	35	3.96	4.88	10
Ulmus americana	—	—	5	10	1	10	0.02	6	40	1.78	7	50	7.32	9.12	13
Carya cordiformis	50	5	5	10	1	5	0.01	2	20	0.31	2	15	1.55	1.87	2
Acer negundo	25	3	10	10	—	—	—	—	—	—	1	5	0.36	0.36	3
Tilia americana	—	—	—	—	—	—	—	—	—	—	3	10	1.72	1.72	5
Acer saccharum	200	10	100	55	7	40	0.26	9	55	1.57	—	—	—	1.83	35
Quercus rubra	—	—	5	5	—	—	—	1	5	0.06	1	10	1.63	1.69	9
Fagus grandifolia	—	—	53	10	1	10	0.03	1	5	0.11	1	10	0.73	0.87	6
Liriodendron tulipifera	—	—	3	5	—	—	—	—	—	—	1	5	1.67	1.67	1
Quercus palustris	—	—	—	—	—	—	—	—	—	—	1	10	1.52	1.52	1
Acer rubrum	100	7	—	—	2	15	0.07	7	30	1.58	2	20	2.72	4.37	12
Betula nigra	—	—	—	—	—	—	—	1	10	0.31	1	5	0.61	0.92	1
Total							0.39			6.64			23.76	30.82	

TABLE 2. *Data for tree species of stands located on the outer flood plain and Mertensia "island". For explanation see table 1.*

	Less than 1″ d.b.h.				More than 1″ d.b.h.										
	Less than 1′ tall		More than 1′ tall		1–3.9″			4–9.9″			More than 10.0″			Total BA	C
	D	F	D	F	D	F	BA	D	F	BA	D	F	BA		
Outer Flood Plain															
Fraxinus americana	—	—	5	10	1	5	0.01	1	10	0.11	2	20	4.97	5.09	7
Ulmus americana	—	—	3	5	6	20	0.10	1	10	0.14	—	—	—	0.24	4
Carya cordiformis	75	7	10	10	—	—	—	—	—	—	—	—	—	—	1
Acer negundo	100	10	125	50	8	40	0.25	1	10	0.31	1	5	0.36	0.92	9
Tilia americana	—	—	5	5	4	5	0.06	2	20	0.64	2	10	4.21	4.91	9
Acer saccharum	125	10	665	90	21	65	0.31	3	20	0.45	—	—	—	0.76	28
Ulmus rubra	—	—	65	50	10	35	0.16	1	10	0.24	1	10	1.39	1.79	14
Quercus rubra	—	—	3	5	—	—	—	—	—	—	—	—	—	—	—
Celtis occidentalis	—	—	—	—	1	5	0.01	—	—	—	—	—	—	0.01	—
Fagus grandifolia	—	—	25	40	2	15	0.03	2	20	0.86	3	25	3.89	4.78	50
Liriodendron tulipifera	—	—	5	10	2	10	0.03	—	—	—	2	15	5.89	5.92	24
Quercus alba	—	—	—	—	—	—	—	—	—	—	1	5	2.34	2.34	5
Acer platanoides	—	—	—	—	1	5	0.01	—	—	—	—	—	—	0.01	—
Platanus occidentalis	—	—	—	—	—	—	—	—	—	—	1	10	0.91	0.91	1
Total							0.97			2.75			23.96	27.68	
Mertensia "island"															
Fraxinus americana	—	—	3	5	2	15	0.02	3	15	1.34	5	45	6.95	8.31	26
Ulmus americana	—	—	—	—	1	5	0.04	—	—	—	—	—	—	0.04	—
Carya cordiformis	—	—	—	—	—	—	—	1	10	0.28	—	—	—	0.28	7
Acer negundo	25	3	60	45	6	35	0.16	1	5	0.43	—	—	—	0.59	9
Tilia americana	—	—	5	5	5	15	0.10	1	5	0.09	—	—	—	0.19	5
Ulmus rubra	—	—	—	—	3	25	0.09	3	15	0.76	5	15	5.18	6.03	45
Celtis occidentalis	—	—	15	15	4	20	0.07	2	15	0.50	6	45	12.03	12.60	37
Quercus palustris	25	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Juglans nigra	—	—	—	—	—	—	—	—	—	—	1	10	1.15	1.15	14
Total							0.48			3.40			25.31	29.19	

being present on the outer flood plain (1% cover), the inner flood plain (3% cover), and the terrace (4% cover). The other two were present only on the terrace: flowering dogwood (*Cornus florida*) with 1% cover and hawthorn (*Crataegus* sp.) with less than 1% cover.

The forest of the terrace, which is above the flood level, had a practically closed canopy (7% unoccupied space). Within the forest only two species, sugar maple (*Acer saccharum*) and basswood (*Tilia americana*), were present in all size classes (table 1). The sugar maple was by far the most vigorously reproducing tree. Red oak (*Quercus rubra*) and bitternut hickory (*Carya cordiformis*) were absent in only the small tree (1–3.9″) class and

TABLE 3. *Per cent shrub, sapling, and liana cover based on measurements along 400 meters of line transect in each stand.*

	Outer flood plain	Mertensia "island"	Inner flood plain	Terrace
	50	41	66	79
Unoccupied space				
Shrubs				
Lindera benzoin	54	67	33	6
Berberis thunbergii	< 1	—	1	—
Viburnum prunifolium	< 1	—	—	3
Ilex laevigata	—	—	3	—
Rubus sp.	—	< 1	3	—
Cephalanthus occidentalis	—	—	1	—
Staphylea trifolia	—	17	—	—
Evonymus atropurpureus	—	< 1	—	—
Lianas				
Rhus radicans	5	12	2	—
Parthenocissus quinquefolia	< 1	1	—	—
Lonicera japonica	2	—	1	7
Vitis cordifolia	—	1	—	—
Tree saplings (15 species)	55	4	16	84

both had a good number of seedlings and saplings. The other species present were either those represented by large trees with little or no reproduction, white ash (*Fraxinus americana*), black oak (*Quercus velutina*), and shagbark hickory (*Carya ovata*), or by seedlings and saplings, box-elder (*Acer negundo*) and black walnut (*Juglans nigra*). Although ash had the highest total basal area, nearly all was contributed by individuals of the largest size class. Red oak was similar to the ash in distribution of basal area, but the sugar maple differed from them in having more basal area in the smaller size classes.

The forest of the inner flood plain had a canopy only slightly less closed than that of the terrace (11% unoccupied space). The two species that occurred in all size classes were the red maple and the bitternut hickory. However, the American elm and beech were absent only in the seedling class,

the white ash only in the young tree (1–3.9″) class and the sugar maple only in the largest size class. Present as large trees but failing to demonstrate capacity for self-perpetuation in the community were the basswood, box-elder, tulip tree, pin oak and river birch. The elm made the largest contribution to total basal area with the ash second. Most of this was in the 10″ and over size class. Red maple with more participation by the smaller size classes was third in its contribution to basal area. Not in the sampling data but present in the area were swamp white oak (*Quercus bicolor*) and black gum (*Nyssa sylvatica*).

The shrubs and lianas of the inner flood plain were somewhat more important than they were in the vegetation of the terrace. However, unoccupied space in this layer measured 66% (table 3), so that appreciably less than half of the ground was covered. Five species of shrubs and two species of lianas occurred, with spicebush (*Lindera benzoin*) furnishing practically all of the cover, none of the others contributing over 3% (table 3). Saplings contributed less than half as much cover as the shrubs. Three species, red maple, American hornbeam and red oak, not in the sapling quadrat data occurred on the transect lines for the shrub layer.

The forest of the outer flood plain occupies deep, alluvial soil. Being somewhat higher than the inner flood plain it is flooded for shorter periods. In addition both surface and subsurface drainage are good in striking contrast with the inner flood plain, and its surface is not so intensely subjected to scouring erosion as that of the inner flood plain.

One species only, box-elder, ocurred in all size classes. Sugar maple occurred in all but the largest size class. Three others, ash, slippery elm (*Ulmus rubra*) and beech, were in all but the seedling class. A few, white oak (*Quercus alba*), tulip tree (*Liriodendron tulipifera*), and sycamore (*Platanus occidentalis*) were present primarily as large trees with little or no representation in reproduction classes. Large individuals of shagbark hickory also were seen in the stand although none occurred in the quadrats. In contrast, bitternut hickory (*Carya cordiformis*) was vigorous in the smaller size classes. The bulk of the forest consisted of tulip tree, ash, beech, and basswood which contributed most of the basal area. In the smaller size classes, however, the beech, sugar maple and basswood were most important. The largest tree on the outer flood plain was an ash 38″ d.b.h. Honey locust (*Gleditsia triacanthos*), although not present in the quadrat data, occurred on the site.

The shrub layer was much better developed here than in either the inner flood plain or the terrace, only half of the layer was unoccupied by shrubs, lianas or saplings. There were three species of shrubs and three of lianas. Spicebush was again of greatest importance and practically the only shrub of any importance. Japanese barberry (*Berberis thunbergii*) and black haw

(*Viburnum prunifolium*) occurred but contributed an insignificant amount to the cover. Poison ivy (*Rhus radicans*) and Japanese honeysuckle (*Lonicera japonica*) were the two principal lianas (table 3). Eleven saplings contributed to cover in this layer, with the sugar maple contributing 30%, which was by far the most. Hornbeam, hackberry (*Celtis occidentalis*) and black walnut, not present in the quadrat data, occurred in the stand and contributed small amounts of cover as saplings on the transect measurements of the shrub layer.

The forest of Mertensia "island", which is farther downstream, also occupies deep, alluvial soil which is subject to flooding. It also possesses good surface and subsurface drainage, so it is not subject to extended periods of saturation in the upper soil horizons. Deposition, not erosion, is characteristic of its surface. No tree species occurred in all size classes although presumably intensive search or more intensive sampling might place some in this category. This might be true of white ash and hackberry which were not present in any of the small quadrats in which seedlings were sought. The most aggressively reproducing tree was box-elder but none of its individuals had reached the largest size class. Three species, hackberry, white ash and slippery elm form the bulk of the forest, contributing most of the basal area. Cover measurements agree with the basal area measurements in indicating these three species as primarily important. Four species not sampled in the quadrats occurred on the transect line: sycamore (5% cover), hawthorn (2% cover), hornbeam (1% cover) and white mulberry (*Morus alba*) (1% cover). Open space in the tree canopy was about 11%. Among the many large trees, the largest was a hackberry measuring 40" d.b.h.

The shrub layer was denser (unoccupied space only 4%) than in any of the stands previously discussed. Spicebush reached its best development here but along with it bladdernut (*Staphylea trifolia*) was very important. Poison ivy also produced much more cover than in any of the other stands. Compared with the other stands, the contribution to cover by saplings was low, corresponding to the lower count of saplings on the quadrats. Only three species, hackberry (2%), box-elder (2%), and bitternut hickory (1%), contributed to cover in the shrub layer.

Discussion. The vegetation of the terrace is apparently in the process of becoming relatively stabilized as a predominantly maple-beech-basswood forest. The presence of black oak, shagbark hickory, and white ash primarily in the larger size classes and their failure to reproduce in contrast with the increasing importance of sugar maple, beech and basswood indicates the change toward the dominance of the last three. This situation is suggestive of more open conditions in the recent past. The area certainly had been cut over in the past, as evidenced by the sprout origin of the oaks, and

probably had been pastured. Some of the tree species other than sugar maple and basswood may be successful in perpetuating themselves but they will be outnumbered by the maple and basswood. The relatively open shrub layer which is in striking contrast with the shrub layer of the flood plain communities on the one hand and the more upland forests of this region on the other hand can be ascribed to the heavy shade produced by the dominants. Low light intensity as the cause of the suppression of the shrub layer is suggested at points where an opening in the canopy has resulted from a fallen tree; here a burst of shrub and sapling growth producing a local thicket is in remarkable contrast to the rest of the stand. Flowering dogwood occurs but is too sparse to form a distinct understory tree layer such as is common in the upland oak forests (Bard 1952, Cantlon 1953). The terrace, lying just above the flood plain, is a distinctly mesic site where moisture conditions are especially favorable. This explains in large part the rapid succession from oak-hickory dominance to maple-basswood dominance. This is in contrast to the oak-hickory forest of the region in general where evidence of such a succession is often entirely absent.

The inner flood plain forest is relatively heterogeneous since small undrained sloughs and low ridges and moderately well-drained sloughs produce variable conditions. This affects areal distribution of reproductive stages and consequently the mature plants too. Sugar maple, red maple, bitternut hickory, ash, and beech are more or less equally successful. Their apparent success is indicative of their increasing importance in the future forest if it is left free of disturbance. The absence of elm seedlings at the time of the survey may not be a consistent character. Another year perhaps they would be common. At any rate all other size classes of the elm are present but in numbers that would lead one to believe that this tree will decrease in importance as time goes on. Its present primary importance as a large tree may date back to an earlier time when the elm got established in numbers along with the box-elder, the red and pin oaks, the river birch and the tulip tree which are all failing to maintain themselves in the community now. The pronounced differences between this community and that of the terrace must be due both to the periodic flooding and to the undulating ground with its poorer drainage and surface conditions. The vegetation on this inner flood plain cannot be presumed to exemplify that of the inner flood plain in general since this particular inner flood plain is characterized by erosion. Deposition more often predominates. Very different conditions prevail where deposition rather than erosion is the rule.

The sites near the river at Burnt Mills and at Raritan, the outer flood plain and Mertensia "island", are very similar. Both have deep alluvial soils that drain rapidly after flooding. Water supply is always adequate especially for the deep-rooted species. Both sites support a mixed forest.

They have no one or two dominants, nor does the reproduction indicate that such a situation is developing. Certain species like sycamore and white oak, which are present in the larger size classes only, might be indicative of earlier disturbance. However, their presence might also be indicative of normal local catastrophe characteristic of the flood plain habitat. The high reproductive potential of both the shade tolerant sugar maple and the intolerant box-elder is indicative of the instability and variable surface conditions of the flood plain habitat. It seems likely that the shade tolerant beech, sugar maple, basswood, and bitternut hickory may gain in proportion to the others but the forest seems destined to remain a mixed one.

Perpetuation of a mixed stand is even more pronounced on Mertensia "island" than on the outer flood plain. On both sites catastrophe, characteristic of flood plains, seems to be capable of maintaining the variety of conditions conducive to the regeneration of species of diverse requirements. Fallen trees, resulting in open places in the canopy, were frequent.

The outer flood plain type of site along the Raritan River is exceedingly favorable for species that can withstand a certain amount of flooding. The trees grow rapidly and attain large size. Potentially the site will support as luxuriant a forest as can grow in this climate. A part of the splendor of the forests is the fine display of spring flowering herbs that is surpassed nowhere else in New Jersey. Such excellent growth and variety of tree species is generally characteristic of flood plain forests of the deciduous forest region (Cowles 1901, Lee 1945, Nichols 1916, and Oosting 1942).

The small remnants of the flood plain woodlands now left are indicative of the splendid forests that must once have covered all of the flood plains of the Raritan River system. Perhaps they will again be more extensive since the values of natural areas are being increasingly recognized today. There is a good chance that the plans now being made for a park system along portions of the Raritan flood plain will include natural reservations where flood plain forests will be allowed to develop again to their natural grandeur.

SUMMARY

1. Evidence from the one example studied indicates that the low terraces that lie just above the flood level of the Raritan River can support a forest dominated by sugar maple, beech, and basswood. Their two principal but minor associates will be red oak and bitternut hickory.

2. The flood plains will support forests that are much more varied in composition.

3. The part of the flood plain farthest from the river, the inner flood plain, is less well drained than the part adjacent to the river. The inner flood plain forest which was investigated in this study occupies a site where

surface erosion at flood times scours the ground resulting in an uneven surface. Sugar maple, red maple, ash and beech as a group are becoming dominant in place of the earlier established elm, box-elder, red oak, basswood, pin oak, river birch and tulip tree. This succession cannot be presumed for the inner flood plain of the river as a whole because more often deposition rather than surface erosion occurs during flooding and the conditions then are exceedingly different. No extensive relatively undisturbed stands occur on the latter type of site.

4. The outer flood plain sites or broad more or less level areas of deposition next to the river have a deep, well-drained soil and support a deciduous forest of mixed composition in which no convincing trend toward the dominance of a few species is evident.

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A NEW SPECIES OF RHOPALOMYCES OCCURRING IN FLORIDA

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About 25 days after they had been planted with portions of softened stem or root of bean (*Phaseolus vulgaris* L.) seedlings kindly collected by W. D. Moore near Fort Lauderdale, Florida, on February 17, 1953, more than a dozen maizemeal-agar plate cultures began to show development of a species of *Rhopalomyces* apparently different from any congeneric form hitherto described. The fungus must presumably have originated from Florida, for the seedlings had been received at the Plant Industry Station in a tightly wrapped package, and after the wrapping had been removed the specimens were given adequate protection against contamination by microorganisms in the laboratory. In preparing the young plants for the isolation of any root-rotting oomycetes that might have caused the softening of their cortex they had not been subjected to surface disinfection. Mycelium of *Pythium spinosum* Sawada (1927) had promptly grown out from all the pieces of seedling tissue. Soon various eelworms and rhizopods had multiplied actively in the cultures, with the result that after approximately 10 days predacious and parasitic fungi destructive to these animals had developed increasingly. Different kinds of saprophytic fungi thereupon also came to light, among them being the new *Rhopalomyces,* which arrested attention by bearing its spores distally in a striking hemispherical arrangement; the lower half of the enlargement at the tip of each conidiophore remaining nude and exposed to view (fig. 1, a). A term having reference to its characteristic half-covered appearance may serve as an appropriate epithet for the fungus.

Rhopalomyces semitectus Drechsler sp. nov. Oculo nudo inconspicuus; fertilibus hyphis rigidis, erectis, fuligineis, plerumque raris, vulgo solitariis sed interdum bigeminis, saepe 800–1000 μ altis, magnam partem cylindricis et 9–12 μ latis, apice in caput sporiferum latescentibus; sporifero capite obovoideo, saepe 65–70 μ longo, 45–53 μ lato, deorsum nudo, sursum in apicibus multorum sterigmatum multa (saepe 110–150) conidia ferente; sterigmatis verruciformibus, 2.5–4 μ altis, 2–3 μ latis; conidiis fuligineis, irregulariter elongato-ellipsoideis, 25–35 μ longis, 7–9 μ latis.

Habitat in radicibus *Phaseoli vulgaris* putrescentibus prope Fort Lauderdale, Florida.

Uusually inconspicuous to the naked eye; conidiophores rigid, erect, light brown, mostly rather sparsely scattered, commonly solitary but sometimes arising in pairs, often 800 to 1000 μ high, for the most part 9 to 12 μ wide,

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widening distally into a sporiferous enlargement; sporiferous enlargement obovoid, often 65 to 70 μ long and 45 to 53 μ wide, beset on the distal or hemispherical surface with many (often 110 to 150) wart-like protuberances, commonly 2.5 to 4 μ high and 2 to 3 μ wide, on each of which a single conidium is borne radially; conidia light brown, somewhat irregularly elongate ellipsoidal, 25 to 35 μ long, 7 to 9 μ wide.

Occurring in decaying roots of *Phaseolus vulgaris* near Fort Lauderdale, Florida.

The obovoid shape of the sporiferous enlargement in *Rhopalomyces semitectus* and the development of conidia only on the distal hemispherical surface would seem to distinguish the Florida fungus sufficiently from all congeneric forms known. In Corda's (1839, pl. 2, fig. 3, 4) impressive illustrations of his *R. elegans*, on which species the genus was erected, the terminal enlargement is of subspherical form, and is everywhere beset with sterigmata. Spherical shape of the sporiferous enlargement and distribution of sterigmata everywhere on its surface are evident also in an illustration that Costantin (1888, p. 37, fig. 5: 1, b) gives of his *R. nigripes*. Thaxter (1891) describes the large head of his *R. strangulatus* as being perfectly spherical and in an accompanying figure (1891, pl. 3, fig. 5) shows sterigmata everywhere on its surface. Berlese (1892) characterizes the "vesicula" of his *R. magnus* as "perfecte globosa," and in a relevant illustration (Berlese 1892, pl. 10, fig. 27) shows sterigmata arranged about as closely on its proximal surface as in its equatorial and distal regions. The "vesicula" of *R. macrosporus* Marchal (1893) likewise is set forth as being spherical and as bristling with sterigmata over its entire surface.

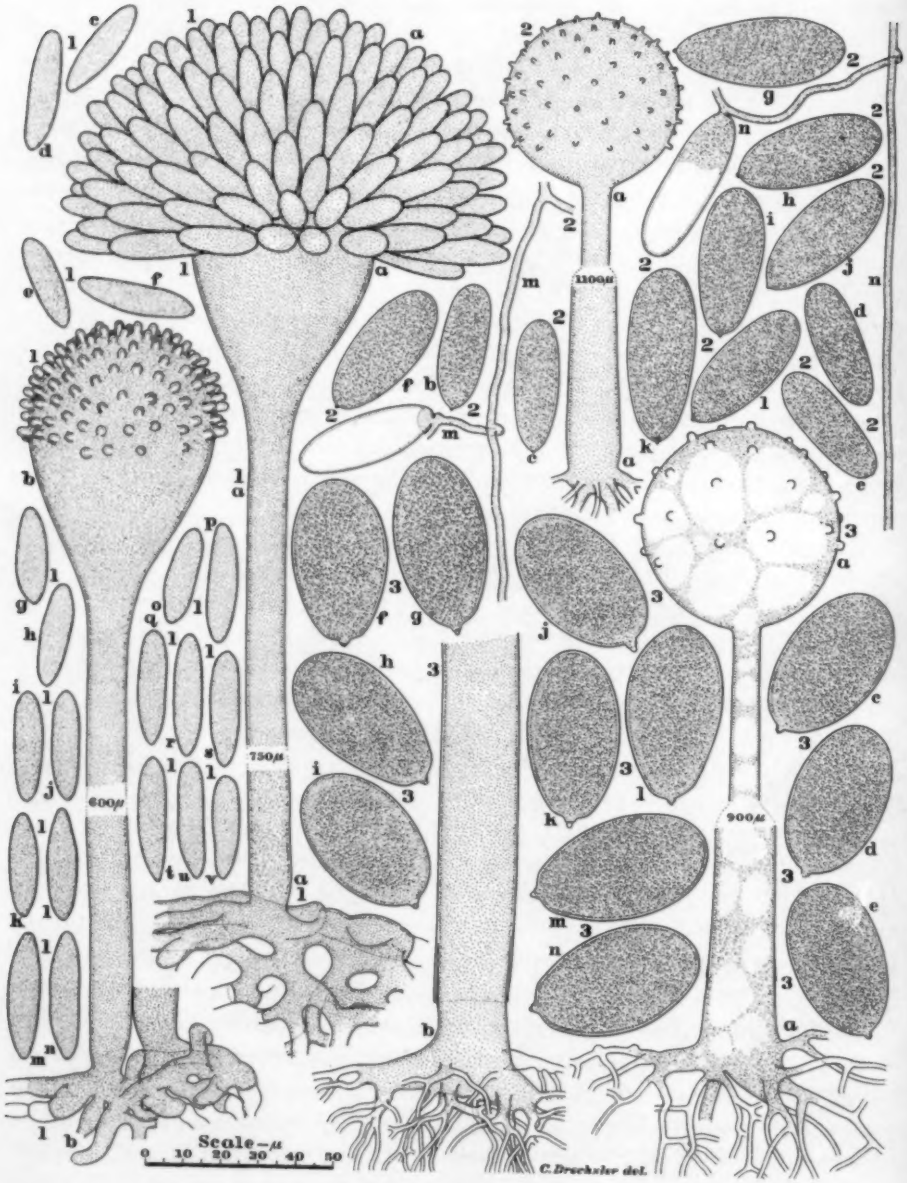
In the Petri plate cultures I have prepared for many years by planting discolored roots or decaying vegetable detritus on maizemeal-agar plates 2 species of *Rhopalomyces* have developed repeatedly, one of them (fig. 2, a–n) agreeing tolerably with the description of *R. elegans* and the other (fig. 3, a–n) with that of *R. magnus*. The sporiferous enlargement in both of these species always appears spherical, its circular outline merging abruptly, rather than gradually, with the outline of the supporting shaft (fig. 2, a; 3, a). When a conidiophore in either species reaches full maturity the enlargement is completely concealed within a handsome subspherical mantle of radially arranged conidia. Nevertheless, when in my cultures the mature conidia have fallen off, the denuded head in many instances is found devoid of sterigmata in a proximal zone of readily noticeable extent (fig. 2, a; 3, a). Apparently the proximal barrenness so conspicuous in the terminal enlargements of *R. semitectus* is not wholly alien to *R. elegans* and *R. magnus*, though in these 2 species the barren areas are usually concealed by the conidia directed radially downward from sterigmata found well below the equator of the enlargement.

While in *Rhopalomyces elegans* and *R. magnus* very little mycelium near

the base of a mature sporophore shows pronounced modification, the circumbasal hyphae in *R. semitectus* become widened and colored for distances of 10 to 50 μ. In the empty filaments partitions are visible here and there (fig. 1, a, b), having apparently been laid down, after the manner usual in many phycomycetes, as retaining walls marking successive stages in the evacuation of protoplasm from the subjacent mycelium. Similar partitions were observed by Marchal in old mycelium of *R. macrosporus*. Owing apparently to better anchorage provided through more extensive widening and induration of the circumbasal hyphae in *R. semitectus*, the sporophores of this fungus often remain standing erect for weeks, whereas those of *R. elegans* and *R. magnus* commonly will fall over in a few days. When eventually a sporophore of *R. semitectus* falls over on an agar substratum its relatively thick-walled terminal enlargement usually retains its original shape, and its sterigmata, apparently larger and sturdier than the sterigmata of any known congeneric species, long remain without any visible change. When a sporophore of *R. elegans* or of *R. magnus* topples, its apical enlargement more often collapses or becomes badly deformed, and soon afterwards its sterigmata tend to vanish from sight.

The conidia of *Rhopalomyces semitectus* (fig. 1, c–v) are markedly smaller than those of *R. elegans* (fig. 2, b–l), *R. magnus* (fig. 3, c–n), and *R. macrosporus*. They would seem, in general, somewhat shorter than the conidia of *R. strangulatus*. From the conidia of *R. nigripes*, however, they evidently differ rather little with respect to dimensions. They nearly always present haphazard irregularities of outline and consequently lack the symmetry of form usual in the conidia of congeneric species. Once they are detached their proximal and distal ends are not always readily distinguished. The spores have not so far been seen to germinate.

However, some of my Petri plate cultures in which *Rhopalomyces elegans* developed showed abundant germination of the conidia of that species. Germination here entails, as an initial step, the yielding of the conidial envelope in a small circular area at the proximal end and adjacent to the hilar scar or protuberance. From the single orifice 2 germ hyphae are extended at a wide angle (fig. 2, m, n). These hyphae, aseptate and mostly 2 to 2.4 μ wide, readily anastomose with the similar germ hyphae (fig. 2, m, n) produced by neighboring conidia. Where numerous conidia germinate in scattered positions an extensive but somewhat scanty mycelium, colorless, continuous, sparsely branched and haphazardly anastomosed, is brought into being. In Petri plate cultures where mature sporophores have toppled over, so that large conidial clusters have been prostrated on the moist agar substratum, the many germ hyphae extended from all conidia in a cluster may anastomose to form a single closely-knit unit that soon sends up a new conidiophore bearing a new head of conidia. Thus, through simultaneous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germination and abundant fusion of germ hyphae, repetitional reproduction not of individual spores but of capitate spore clusters is spectacularly achieved.

In setting forth his view that *Rhopalomyces magnus* did not differ enough from *R. elegans* to merit recognition as a separate species Marchal stated that Thaxter had ascribed to *R. elegans* dimensions as large as those of *R. magnus*. This statement appears not strictly true with respect to conidial width. Thaxter (1891) from observations on various substrata, including bones, dung, potatoes and squash rind, gave 35–55 × 11–22 μ as the spore dimensions of Corda's species; whereas in the diagnosis of *R. magnus* spore measurements of 48–52 × 25 μ were given. In my culture the conidia of the species herein identified as *R. magnus* have commonly been 45 to 51 μ long and 24 to 28.5 μ wide. Although Berlese characterized the conidia of *R. magnus* as being minutely papillate at the base, the basal protrusion in conidia of the American fungus (fig. 3, c–n) considered as belonging to this species is decidedly wider and more prominent than the hilar protuberance often noticeable in the narrower conidia held referable to *R. elegans* (fig. 2, b-1). The sporophores in my material of *R. elegans* usually bear about 100 conidia, whereas three mature sporophores selected at random in my cultures of *R. magnus* were found to have produced 38, 42, and 46 conidia, respectively.

In widening out gradually into its obovoid terminal enlargement the sporophore of *Rhopalomyces semitectus* presents especially strong contrast with the sporophore of *R. strangulatus*, which becomes sharply constricted into a slender neck before swelling abruptly to form a very massive spherical head. As the original description of *R. strangulatus* sets forth the sporophores as being pure white, but does not state whether the spores borne on them are colorless, colored or dark, Berlese suspected that the conidia were probably hyaline, and accordingly proposed that the fungus be excluded from Corda's genus. The proposal, though with some justification at the time, apparently was not urged further and may well have been abandoned after Thaxter (1903, p. 102) stated that all species of *Rhopalo-*

FIG. 1. *Rhopalomyces semitectus:* a, sporophore laden with conidia; b, denuded sporophore; c–v, random assortment of detached conidia. FIG. 2. *Rhopalomyces elegans* as found in a maizemeal-agar plate culture planted with a diseased lupine (*Lupinus* sp.) seedling taken from a greenhouse near Beltsville, Maryland, in February, 1950: a, denuded sporophore; b-l, detached conidia; m, n, two conidia with germ hyphae that have anastomosed with other germ hyphae. FIG. 3. *Rhopalomyces magnus:* a, denuded sporophore produced in a maizemeal-agar culture planted with vegetable detritus collected near Greeley, Colorado, in September, 1943; b, base of sporophore found in a Petri plate culture planted with a small quantity of decaying potato (*Solanum tuberosum* L.) leaves collected near Presque Isle, Maine, in October, 1943; c–e, conidia from the Colorado culture; f–n, conidia from the Maine culture. Owing to lack of space median portions of indicated lengths are omitted from the sporophores shown in figure 1, a; figure 1, b; figure 2, a; and figure 3, a. All figures × 500.

myces have dark spores. Thaxter's extraordinarily large fungus may appear less incongruous with other members of the genus by considering its resemblance to a much more commonplace species that developed very sparingly in a maizemeal-agar plate culture that had been planted with a small quantity of leaf mold collected in deciduous woods near Park Falls, Wisconsin, on November 17, 1954.

When the Wisconsin fungus came under observation all of its sporophores, only 16 in number, had already toppled over on the moist agar substratum. They appeared uniformly of medium brown color. Individually they consisted in large part of a hyphal shaft, about 1 millimeter long, that from the base almost to the tip commonly varied between 15 and 19 μ in diameter (fig. 4, a). In each sporophore, however, a distal portion, usually

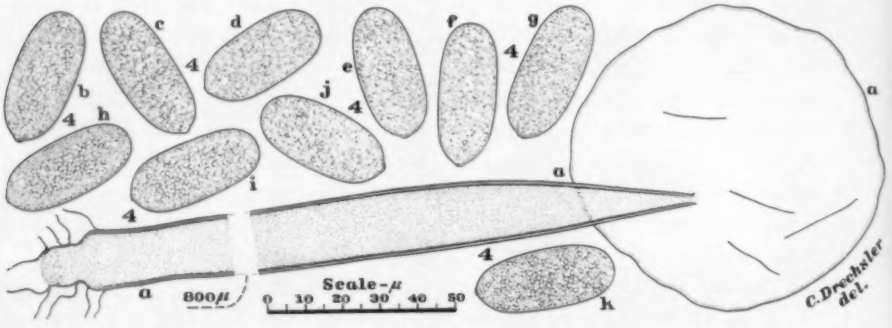

FIG. 4. *Rhopalomyces* sp. obtained from Wisconsin material: a, prostrate sporophore with collapsed membranous envelope of denuded terminal enlargement flattened on substratum; b–k, detached conidia, showing usual variations in size and shape. Owing to lack of space a median portion 800 μ long is omitted from the sporophore shown in figure 4, a. All parts $\times$ 500.

60 to 75 μ long, tapered upward to a width of 2.5 μ at the junction of the tubular neck with the globose enlargement, thereby presenting distinctive parallelism with the less gradual constriction characteristic of *Rhopalomyces strangulatus*. Unfortunately the terminal enlargement had collapsed in all instances, but since its flattened envelope measured usually about 80 μ across, the diameter of the head in a living state may have been approximately 55 μ. Strewn thickly around the collapsed enlargements were numerous dark brown conidia with hemispherically rounded ends (fig. 4, b–k). These spores measured 25 to 28 μ in length and 15 to 18 μ in width. Except for a slight basal protuberance, they showed individually a smooth symmetrical outline. They revealed somewhat indistinctly the rather minutely globulose internal structure often observable in conidia of *R. elegans* and *R. magnus*. The fungus thus appeared unquestionably referable to Corda's genus.

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THE INTERRELATIONSHIP BETWEEN ORTHIC TETRAKAIDECAHEDRA AND RHOMBIC DODECAHEDRA IN AGGREGATION SERIES[1]

YVONNE R. NAUM AND EDWIN B. MATZKE

For over a hundred years the rhombic dodecahedron was generally accepted as a fundamental shape for morphologically undifferentiated cells in tissues. This conclusion was arrived at to a considerable extent because of the emphatic disquisitions of Kieser (1815, 1818). Subsequently Lewis (1923), examining cells in three dimensions for the first time, proved that the dodecahedral concept was incorrect. In effect he substituted the orthic tetrakaidecahedron of Lord Kelvin (1887) with fourteen faces, of which eight are regular hexagons and six are squares. Extensive researches by various authors have since shown that the Kelvin figure is only rarely approximated in actual cells, although the average number of faces of cells in essentially undifferentiated tissues is close to fourteen. These two polyhedra, the dodecahedron with twelve faces and the tetrakaidecahedron with fourteen, have thus been the two fundamental types around which discussions of cellular configurations have largely centered.

Marvin (1936) studied the aggregation of orthic tetrakaidecahedra. He showed that when they are stacked regularly in layers, 14 surround a central one in the first layer, 50 fit around these 14 in the second layer, and 110 comprise the third layer. This is according to the formula $T_n = 12n^2 + 2$, in which T_n is the number of units in any given layer, and n is the number of the layer.

When tetrakaidecahedra are stacked in this way, in regular layers, the aggregate mass takes on the form of a rhombic dodecahedron. Although this is most apparent in the third layer (fig. 6), it can be seen also in the second (fig. 5) and even in the first layer (fig. 4). The orthic tetrakaidecahedra shown in figures 4–6 were constructed of stiff paper as previously described (Matzke 1931).

The faces of the rhombic dodecahedron thus formed are regular and equal (figs. 4–6), and follow a definite succession. They are represented in the orthic tetrakaidecahedron by the common edges between two hexagonal faces, of which there are 12 (fig. 1). The six four-rayed vertices of the

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It is a pleasure to acknowledge the generous help of Professor Frank G. Lier in the photographic work involved. The manuscript was critically reviewed by Professor James W. Marvin, and his helpful suggestions are much appreciated.

dodecahedron (fig. 2) are represented by the square faces of the tetrakaidecahedron (fig. 1), and the eight three-rayed vertices of the dodecahedron by the hexagons of the tetrakaidecahedron.

In the first layer (fig. 4), in which 14 tetrakaidecahedra surround a central one, each of the 12 faces of the rhombic dodecahedron is made up of parts of four tetrakaidecahedra which are shaded gray. Each tetrakaidecahedron contributing a square gray face forms a part of four faces of the dodecahedron, and thus constitutes one of six four-rayed vertices of the dodecahedron; each contributing a hexagonal gray face is shared by three rhombic faces, and constitutes one of eight three-rayed vertices of the dodecahedron. This relationship can be seen also in figure 7. Since there are

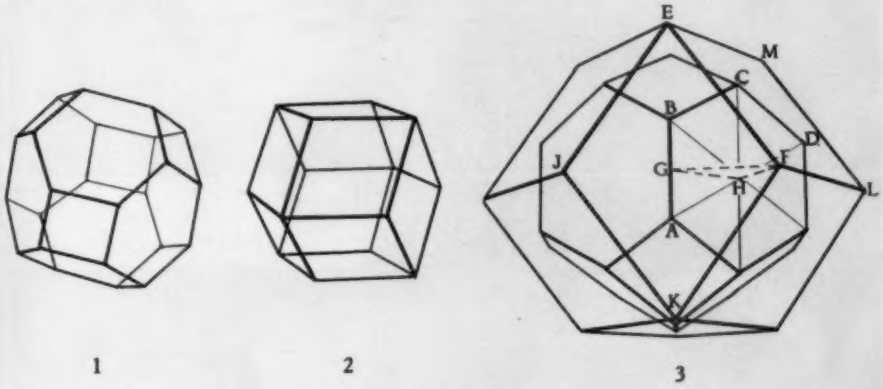

FIG. 1. Drawing of an orthic tetrakaidecahedron showing the 8 regular hexagonal and 6 square faces. This is oriented in approximately the same position as the central tetrakaidecahedron, within the mass, in figures 4, 5, and 6. FIG. 2. Drawing of a rhombic dodecahedron showing the 12 rhombic faces. This is oriented in approximately the same position as the rhombic dodecahedron formed by the aggregate mass of tetrakaidecahedra in figures 4, 5, and 6. FIG. 3. Drawing of a portion of the models shown in figure 7. Explanation in the text.

12 rhombs in all, each made up of portions of four tetrakaidecahedra, half of which (24) are shared by three, and half by four, the total number of tetrakaidecahedra in this layer is 8 + 6 or 14. The four sides of each of the 12 rhombs of the dodecahedron are each composed of two tetrakaidecahedra in this layer. The line of contact between two gray hexagonal faces in figure 4 is directly above the edge between two hexagonal faces of the central tetrakaidecahedron.

In the second layer (fig. 5) 50 tetrakaidecahedra surround the 14 of the first layer. Of these, one (shaded gray) is in the center of each of the 12 rhombs; it rests in the concavity shaded gray in figure 4. Furthermore, the exposed edge between the two hexagonal faces of the gray tetrakaidecahedron in figure 5 is directly above a similar edge of the original tetra-

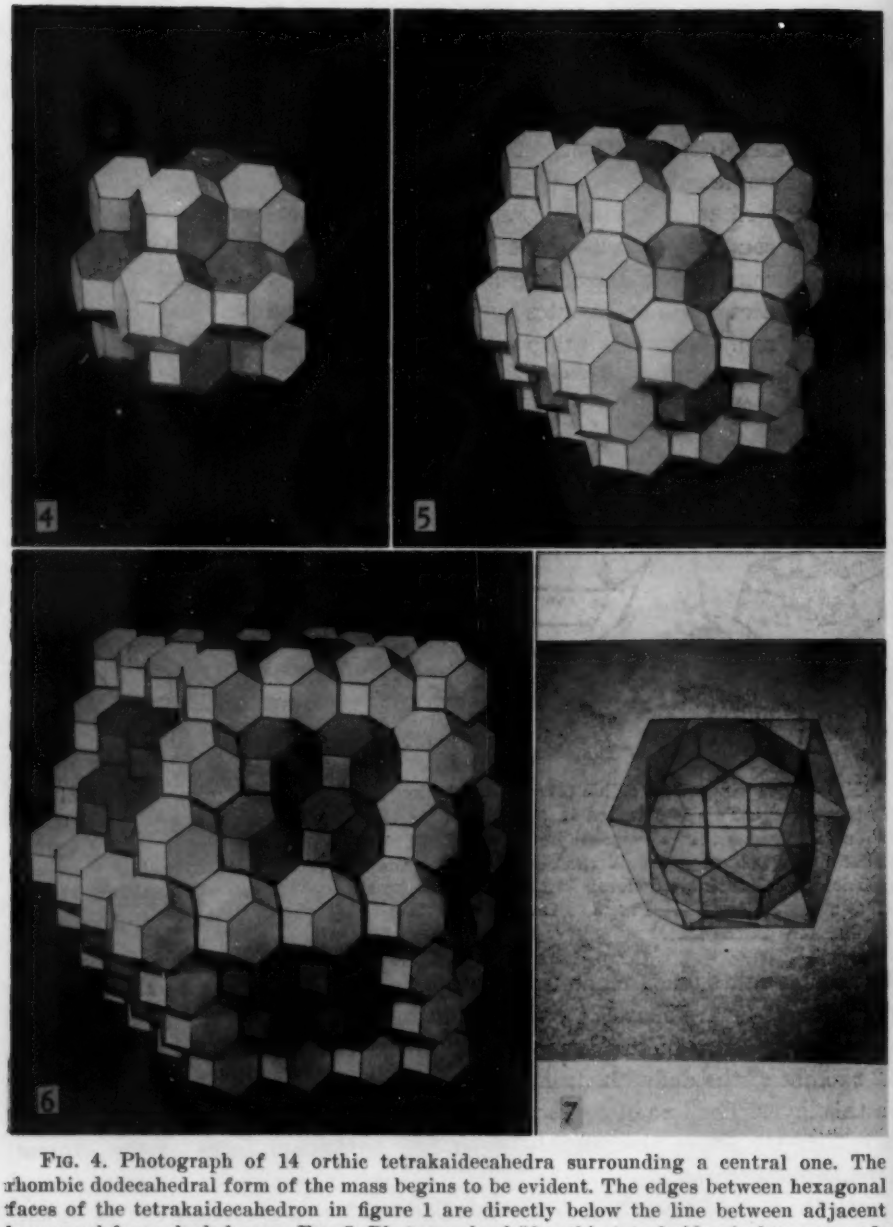

FIG. 4. Photograph of 14 orthic tetrakaidecahedra surrounding a central one. The rhombic dodecahedral form of the mass begins to be evident. The edges between hexagonal faces of the tetrakaidecahedron in figure 1 are directly below the line between adjacent hexagonal faces shaded gray. FIG. 5. Photograph of 50 orthic tetrakaidecahedra surrounding the 14 in figure 4. A gray tetrakaidecahedron is in the center of each of the 12 rhombs of the dodecahedron formed by the mass, and it rests in the concavity shaded gray in figure 4. FIG. 6. Photograph of 110 orthic tetrakaidecahedra surrounding the 50 in figure 5. Four tetrakaidecahedra in the center of each rhombic face are shaded gray. FIG. 7. Photograph of a plastacele model of a rhombic dodecahedron constructed around a similar model of an orthic tetrakaidecahedron. The dimensions are those arrived at according to the calculations in the text.

kaidecahedron in the very center. Four tetrakaidecahedra in each of the 12 rhombs are shared by 2 rhombs, 2 are shared by 3 rhombs, and 2 are shared by 4. The total number of tetrakaidecahedra in this layer is then

$$12\times 1+\frac{12\times 4}{2}+\frac{12\times 2}{3}+\frac{12\times 2}{4}$$

or 50. Each side of the 12 rhombs is bounded in this layer by 3 tetrakaidecahedra.

In the third layer (fig. 6) 110 tetrakaidecahedra surround the 50 of the second layer. Here there are 4 (shaded gray) in the center of each rhomb, and each side of the 12 rhombs is made up of 4 tetrakaidecahedra. Of the 12 tetrakaidecahedra bounding each rhomb, 8 are shared by 2 faces, 2 by 3 faces, and 2 by 4. In this layer there is again a concavity in the very center of each of the 12 rhombs, and the line between two hexagonal gray faces in this concavity is directly above the edge between two hexagonal faces of the original 14-hedron in the center of the whole mass.

In the next layer there would be 9 central (gray) tetrakaidecahedra in each rhomb, and each side of each rhomb would be composed of 5 tetrakaidecahedra, etc.

In order to establish the relationship between the tetrakaidecahedron and the rhombic dodecahedron formed by concentric stacking as outlined above, the dimensions were calculated of a rhombic dodecahedron within which an orthic tetrakaidecahedron is inscribed (fig. 3).

If any edge of the orthic tetrakaidecahedron is x, then AB, BC, CD all equal x (fig. 3). AB and CD are in contact with the faces of the rhombic dodecahedron, $EFKJ$ and $EMLF$, and may be extended to the vertices as the long diagonals, EK and EL, of the rhombic faces. Since angles ABC and BCD are the internal angles of a hexagon, they are 120°. Angles CBE and BCE are therefore each 60°, and EBC is an equilateral triangle. Therefore BE and EC equal BC, and the long diagonals of the rhombic faces of the circumscribed dodecahedron in figure 2 are all $3x$.

The line GH is the apothem of a hexagon and is therefore $\frac{x\sqrt{3}}{2}$ (H being the center of a hexagonal face). The dihedral angle between two hexagonal faces in an orthic tetrakaidecahedron is 109°28′16″ (Matzke 1927). Since FGJ (fig. 3), the short diagonal of a rhombic face, is a straight line, angle FGJ is 180°; then angle $FGH = \frac{180° - 109°28'16''}{2}$ or 35°15′52″. Angle GHF is 90°, and GHF is therefore a right triangle of which the base, GH, is known, and angle FGH is known. Then $\cos \angle FGH = \frac{\frac{x\sqrt{3}}{2}}{GF}$.

$$GF \cdot \cos \angle FGH = \frac{x\sqrt{3}}{2}; \qquad GF = \frac{\frac{x\sqrt{3}}{2}}{.82};$$

$$GF = \frac{.87\,x}{.82}; \qquad GF = 1.06\,x$$

Therefore the short diagonal of the rhomb is $2.12\,x$, and the side of the rhomb is $1.84\,x$. In other words, if any edge of the inscribed tetrakaidecahedron is considered as 1, then any edge of the rhombic dodecahedron is 1.84. Not all of the mathematical considerations involved are analyzed in detail here.

Figure 7 is a photograph of a rhombic dodecahedron circumscribed around an orthic tetrakaidecahedron, both made of plastacele, and both constructed in accordance with the ratios derived above. Approximate measurements of the rhombs in figures 5 and 6 show that their dimensions are similar to those of figure 7.

In a sense, then, the two contrasting "ideal" figures for cells which have been proposed during the last century and a half are brought together. No cell with the shape of the rhombic dodecahedron has ever been reliably described. On the other hand, cells with six quadrilateral and eight hexagonal faces have been found in a considerable number of tissues, although their occurrence is relatively infrequent.

In addition to the importance placed upon the Kelvin tetrakaidecahedra by Lewis, their significance was also emphasized by van Iterson and Meeuse (1941) and Meeuse (1942). The latter authors recorded their occurrence in the tuberous roots of *Asparagus Sprengeri*, the leaf parenchyma of *Rhoeo discolor*, and in other plants. Subsequently, Hulbary (1948) reported orthoid tetrakaidecahedra in two per cent of the cells in the leaf parenchyma of *Rhoeo*, and further research confirmed the presence in these leaves of fairly close approximations to minimal tetrakaidecahedra (Macior and Matzke 1951). The percentage of tetrakaidecahedra with six quadrilateral and eight hexagonal faces is higher in *Rhoeo* than in any other organism thus far studied, and in numerous investigations cells with this configuration did not occur at all.

Unless there are tissues possessing far greater regularity of cellular arrangement than those already analyzed, the possibility seems remote of finding rhombic dodecahedra resulting from the stacking in concentric series of tetrakaidecahedral cells in plants and animals. Nevertheless, the curious combination of the two much-discussed basic "types" for cells, as outlined above, is fundamental to mathematical concepts of aggregation phenomena of cells in tissues.

SUMMARY

1. The two basic "types" which have been proposed and defended for cells in morphologically undifferentiated tissues were first the rhombic dodecahedron (fig. 2) and later the orthic tetrakaidecahedron (fig. 1).

2. When orthic tetrakaidecahedra are stacked in regular layers around a central one, the mass assumes the form of a rhombic dodecahedron (figs. 4, 5, 6).

3. Each rhomb of the dodecahedron is represented, in the tetrakaidecahedron in the center, by the edge between two hexagonal faces, of which there are twelve (figs. 1 and 7).

4. If a rhombic dodecahedron is circumscribed around a tetrakaidecahedron (figs. 3 and 7), and if each edge of the latter is considered as x (fig. 3, AB), then the long diagonal of each rhombic face of the dodecahedron is $3\,x$ (fig. 3, EK), the short diagonal is $2.12\,x$ (fig. 3, JF), and each edge of the dodecahedron is $1.84\,x$ (fig. 3, JE).

5. Rhombic dodecahedra formed by aggregation of tetrakaidecahedra have been neither approximated nor achieved in actual tissues studied, but the combination of these two "types" is fundamental to mathematical concepts of aggregation phenomena of cells in tissues.

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NOTES ON THE GENERIC NAME FOR CORDAITEAN CONES[1]

WAYNE L. FRY[2]

During the course of an investigation on cordaitean cones the writer had the opportunity to review thoroughly the pertinent literature. A paper was found dealing with cordaitean fructifications which had apparently been overlooked by students of the group. The paper has real interest because it presents a form of the name now in use for cordaitean fructifications which is older than the one currently in use.

In order to clarify the taxonomic position of the various genera embracing cordaitean cones it will be necessary to review the historical development of certain pertinent categories erected to hold these fructifications. The various pertinent genera involved in this review are *Antholithus, Antholithes, Anthites, Cordaianthus* and *Cordaitanthus*. The most logical approach is a chronological résumé. Only by this means can the correct position be established.

Antholithus-Antholithes-Anthites. In volume three of the twelfth edition of his Systema Naturae, Linnaeus (1768) used *Phytolithus* as a major category for fossil plants. Associated with this category, but more specific in its reference, is the name *Antholithus* (p. 172). A translation of the Latin text refers to "a copper-like (colored?) spike of grain coming from the habitat Francobergiae in Hassia in gravelly schists (shales?) which are often metallic." These references, although vague, do indicate fossil plant structures of a fructification character.

Brongniart (1822) discussed impressions of flowers at length under the generic name *Antholithes* (pp. 319–320). The flower is described as having a perianth of six parts, three parts in an inner series and three in an outer series. This pattern of arrangement suggests a trimerous flower. In recognition of this similarity the binomial *Antholithes Liliacea* (plate III, figure 7; Brongniart, 1822) is given to the specimen. The index of this work records the genus as *Antholythes*.

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[1] Published by permission of the Acting Deputy Minister, Department of Mines and Technical Surveys.

[2] Geologist, Geological Survey of Canada. The writer acknowledges the aid received from a Cornell-Glasgow Fellowship at Glasgow University during 1950–51. During the tenure of this fellowship several of the citations referred to in this paper were examined for the first time.

Thanks are due Dr. H. P. Banks of Cornell University for his encouragement of this study which is a small portion of a doctoral dissertation written at Cornell University in 1953.

Already three variations of the genus under discussion are found: *Antholithus* Linnaeus, 1768; *Antholithes* Brongniart, 1822 and *Antholythes* Brongniart, 1822. The form *Antholythes* can be ignored as a typographic error. Of the two forms *Antholithus* or *Antholithes,* the latter is probably the correct one. Kirchheimer (1939) is a footnote (p. 24) in Fossilium Catalogus argues against the acceptance of *Antholithus* Linnaeus because in his opinion *Antholithus* cannot be considered a taxonomic unit. It was a general term into which flowers and fructifications of unknown affinities were grouped for reference purposes. Furthermore Brongniart's name conformed to the binomial system of nomenclature when he described and figured *Liliacea* as a species of *Antholithes.* Finally, the date for beginning fossil plant nomenclature is 1820 according to the latest decisions made at the 8th International Botanical Congress in Paris in 1954. All the evidence therefore supports the use of *Antholithes* Brongniart, 1822 in place of *Antholithus* Linnaeus, 1768.

The problem is, however, not yet resolved as the generic meaning of *Antholithes* must be ascertained in order to eliminate it from any possible consideration as a name for true cordaitean cones.

Brongniart (1828) in the "Prodrome d'une Histoire de Végétaux Fossiles" used *Antholithes.* He included it in the Family Liliaceae under flowers. Brongniart (1828) remarks (p. 149) that these fossil flowers were rare and came from Monte Bolca, near Verona, Italy. The sediments are described as "terrain de sédiment supérieur" and are probably Eocene in age. The citation (Brongniart 1828) on page 128 is quoted since a further typographic form of *Antholithes* is introduced:

"V. *Antholithes*
Antholites Liliacea, pl. 3, figure 7
Terrain de sédiment supérieur."

Some doubt regarding various morphological details of these specimens is expressed in this account. Nevertheless this suggestion of vagueness as to the affinity of fructifications similar to and termed *Antholithes Liliacea* is worth noting. The specimens thus far placed in the genus were considered to have been of Tertiary age and bore a striking similarity to monocotyledonous, trimerous, flowers.

Lindley and Hutton (1833–35) in volume two of "Fossil Flora of Great Britain" illustrate a fructification and call it *Antholithes Pitcairniae* (plate 82, fig. 1 and facing text page). This specimen came from shale associated with the Lower Main Coal at Felling Colliery, near Newcastle-on-Tyne. These sediments are considered part of the Middle Coal Series of Pennsylvanian or Upper Carboniferous age. The descriptions include a reference to a calyx enclosing petals and the relationships suggested by Lindley and Hutton are those of the recent genus *Pitcairnia* in the bromelias.

Schimper (1874) in volume three (pp. 419–421) of "Traité de Paléontologie Végétale" segregates into a new genus *Anthites* all fossil floral organs of mono- or dicotyledonous form but lacking definitive taxonomic position or relationship. Schimper began by placing all of the species of *Antholithes* listed on pages 136–138 in volume three of Heer's "Flora Tertiaria Helvetiae" in his genus *Anthites*. These consist of various floral parts such as petals and inflorescences or fructifications but all are without diagnostic characteristics. The segregation of this type of structure into this genus has not been generally followed by later workers.

In general the genus *Antholithes* can be shown to have been utilized as a convenient place in which to put various fructifications and reproductive structures. In addition to the résumé outlined above a few others are cited below.

1. *Antholithes arundites* Berry
   Berry, E. W. 1916. The Lower Eocene Floras of Southeastern North America. U. S. G. S. Professional Paper 91, pl. 112, fig. 6, and text page 350.
   A stout axis bearing a compact cluster of small flowers; possibly a grass.
2. *Antholithes brownii* Berry
   Berry, E. W. 1931. A Flora of Green River Age in the Wind River Basin of Wyoming.
   U. S. G. S. Professional Paper 165, pl. 15, fig. 3 and text page 77.
   A flower of 5 conical united petals; suggestive of the Solanaceae.
3. *Antholithes arberi* Thomas
   Thomas, H. H. 1925. The Caytoniales, A New Group of Angiospermous Plants from the Jurassic Rocks of Yorkshire. Roy. Soc. London, Philo. Trans. v. 213, pl. 14, figs. 33–40 and text page 327.
   A caytonialean fructification now considered as distinctive from angiosperm forms.

The evidence had been accumulating that structures included in *Antholithes Pitcairniae* Lindley and Hutton, 1833–35 (pl. 82, fig. 1) had cordaitean affinities. Goldenberg (1855–62) in "Flora Fossilis Saraeportana" reported the frequent occurrence of *Antholithes Pitcairniae*, so often attributed to palms and bromelias, with *Cordaites*. Schimper (1874) relates that Grand'Eury had discovered inflorescences similar to *Antholithes Pitcairniae* among the mass of leaves of *Cordaites* and still attached to their branches.

Thus it would appear that the genus *Antholithes* Brongniart, 1822 now included a wide array of fructifications and reproductive structures. Certainly the original meaning of including trimerous, monocotyledonous flowers of probably Tertiary age had now been departed from to a considerable degree. The segregation of *Anthites* had not increased the utility of *Antholithes*. The suggestion of certain forms having organic connection with early coniferalean forms necessitated some modification. Obviously a new generic name was needed.

Cordaianthus-Cordaitanthus. The credit for erecting the new genus and to incorporate within it cordaitean fructifications has been consistently ac-

corded to Grand'Eury (1877) in his "Flore Carbonifère du Département de la Loire et du Centre de la France"—(Part I—Botany) where on page 228 he proposed the genus *Cordaianthus*. This genus was to be used for all fructifications, male or female, which could be shown to be of cordaitean affinity. Grand'Eury, however, makes no formal generic designation and the generic description is practically non-existent. One might assume that *Cordaianthus gemmifer* is a type species since it is the first species described following the generic statement but this is a male fructification.

In a paper published by Ottokar Feistmantel (1876) entitled "Versteinerungen der Boehmischen Kohlen Ablagerungen—III" there are discussed fructifications collected from Bohemian coal fields near Stradonitz and Kralup. Feistmantel remarks that over a period of years he had been handling specimens of the type he describes. His father had also collected them and some were in the museum at Prague. Feistmantel states that he wanted to exclude his *Noëggeratheaestrobus*, a fructification having not even the slightest similarity to a cordaitean type (cf. Feistmantel, 1876, pl. 13, fig. 5 with figs. 1–4). This being the case it was necessary for him to create the new genus *Cordaitanthus*. He remarks that it would not be worth while to make more than one species and hence all of his similar cordaitean fructifications would be placed in one species, *Cordaitanthus communis* O. Feistmantel, pl. 13, figs. 1–4. Two species of *Antholithes* were placed in synonymy by him. They are *Antholithes triticum* Andrae and *A. Pitcairniae* L. & H. He concludes by remarking that his specimens are generally similar to *A. Pitcairniae* but all further descriptions are to be left to his colleagues. There can be no doubt of the instituting of this genus and species by O. Feistmantel in 1876 as he has done it in a formal and concise manner.

Discussion. Having made certain that no claim can be made that *Antholithes* need be considered a generic category for cordaitean fructifications it now becomes necessary to resolve the problem of *Cordaitanthus* O. Feistmantel, 1876 and *Cordaianthus* Grand'Eury, 1877. The preponderance of evidence favoring the acceptance of the form *Cordaitanthus* is summarized as follows:

1. Prior date of publication of *Cordaitanthus* in 1876.
2. Formal indication of the new genus as having cordaitean affinity.
3. Illustration of the new genus and the single species.
4. Citation of synonymy of *Antholithes Pitcairniae* L. & H. with the new genus and species. This citation while not made as definitive by Grand'Eury (1877) in his account is nevertheless made as a comparison thereby indicating an awareness of both authors of its importance and affinity.

It would appear, however, that Feistmantel should have used the species name *Pitcairniae* and the resulting combination now introduced is:
Cordaitanthus Pitcairniae (L. & H.) pro parte, Fry.

SUMMARY

1. This review has had as its main purpose the establishment of the correct generic name for cordaitean fructifications. Literature pertinent to this problem has been dealt with but the literature study of the subject has not been exhaustive insofar as species and extraneous references to the generic category for these cones.

2. Two facts have thus been established: The genus *Antholithes* has been proven to be in no way correctly concerned with cordaitean fructification. The facts as reviewed above seem to establish clearly the priority of the name *Cordaitanthus* O. Feistmantel, 1876 as the correct genus for cordaitean fructification.

GEOLOGICAL SURVEY OF CANADA
OTTAWA, CANADA

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GROWTH AND DEVELOPMENT OF PRIMARY TISSUES IN AERATED AND NON-AERATED ROOTS OF SOYBEAN[1]

C. N. SUN

Although there is considerable information available on root structure, there are only a few accounts of tissue differentiation in roots (Esau 1940, 1943, 1953; Engard 1944; Goodwin & Stepka 1945; Popham 1947; Williams 1947; Wetmore 1947; Heimsch 1951).

Anatomical studies on the roots of soybean have been few. The present work grew out of an interest on the time, place of origin, and direction of tissue differentiation in aerated and non-aerated primary roots of *Glycine max* (L.) Merrill.

In agreement with earlier investigations, the structure of soybean root contains a tetrarch xylem (Van Tieghem & Douliot 1888, Compton 1912, Bell 1934). The epidermis and endodermis consist of a single layer of cells (Bell 1934). Secondary roots arise in the pericycle at loci opposite protoxylem (Van Tieghem & Douliot 1888). The pericycle is three cell layers thick adjacent to protoxylem and two cell layers thick adjacent to phloem areas (Van Tieghem & Douliot 1888). However, Bell (1934) found that the pericycle consists of a single layer of cells. Perhaps this variation is due to different varieties of plants used for study.

Materials and methods. The primary roots of the Monroe variety of *Glycine max* (L.) Merrill were used in this study. The plants were cultured in aerated and non-aerated four salt solution under controlled illumination and temperature.

Soybean seeds were first soaked for 24 hours in the culture solution. Then, in order to reduce or to eliminate surface contamination, they were treated for five minutes in a dilute disinfectant consisting of one part Chlorox (5.25 per cent sodium hypochlorite by weight) to twenty parts water. This treatment considerably increased the percentage of seeds germinating. The seeds were then placed in "germination crocks." The 1.5 L. crocks were covered with cotton mosquito netting to support the beans and the culture solution level was maintained slightly above the cotton netting in order to keep the seeds moist.

After 5 days, seedlings selected on the basis of uniformity of size and length of primary roots, were transferred from the germinating crocks to quart mason jars. The jars were painted black on the outside. One seedling

[1] This paper is a portion of a Ph.D. thesis submitted to the Graduate School of the Ohio State University, Columbus, Ohio.

was placed in each jar, the root being inserted through a hole in the rubber stopper.

Aerators for both germination crocks and jars were made of 5-cm. pieces of porous carbon tubing. One end of the carbon tube was plugged with a rubber stopper; the other end was attached to an 18 cm. length of glass tubing. These aerators were then connected in parallel to an air line by means of "T" tubes. In the germination crocks, the aerator tubes were inserted through the mosquito netting. In the jars, the aerator tubes were inserted through holes in the rubber stoppers used to support the seedlings.

The plants were cultured in a ventilated room under a bank of twelve 96-inch General Electric, T-8, 4500 White fluorescent tubes. Eighteen 60 watt incandescent bulbs, nine on each side of the bank of fluorescent tubes, were set up to provide supplementary light in the red end of the spectrum. The bank of lights was adjusted to give a light intensity at the top of the plants of 900–1000 foot candles. A photoperiod of 15 hours was maintained throughout the experiments. The temperature of the ventilated room was kept at 16–18° C. from 8 P. M. to 5 A. M. (hours of darkness) and at 22–24° C. from 5 A. M. to 8 P. M. (hours of light).

A culture solution suggested by Meyer (1945) was used. The calculated initial osmotic concentration of the culture solution was 0.5 ± 0.03 atmosphere, with an initial pH of 4.0 ± 0.2. The culture solution was changed once a week.

The root tips were fixed in a solution of 5 cc. formalin, 5 cc. propionic acid, and 90 cc. of 50 per cent ethyl alcohol, under a reduced pressure of 450 mm. of mercury. An ethyl alcohol series was used for dehydrating, and a toluol series for dealcoholation. The root tips were imbedded in rubber paraffin and were cut 10 μ thick. The sections were stained with safranin and fast green according to a schedule suggested by Johansen (1940). Free-hand sections of living roots were also studied.

Polychromed methylene blue (Van Fleet 1950) was used for staining the Casparian strips of the endodermis walls in the free-hand sections. One per cent solution of phlorogluein in 50 per cent alcohol and 25 per cent hydrochloric acid were used as a test of lignification.

Results. External Morphology. The root system of the soybean consists of a primary root and numerous lateral roots arranged in four longitudinal rows along the primary root. The lateral roots first appear at the base of the primary root, i.e., just below the hypocotyl. Initiation of lateral root primordia continues acropetally. No primordia, observable with the naked eye, ever develop within 3 cm. of the root apex. The roots of soybean cultured in aerated solutions differed markedly from those in non-aerated cultures. In the former, the primary roots were much longer, smaller in diameter, and the secondary roots much more numerous.

The difference in length of primary roots became evident within four days. At the end of 14 days, the length of primary roots in the aerated solution was 32.4 cm. as compared with 9.2 cm. for non-aerated plants. Over the three-week period of the experiment, the rate of growth of the primary roots in the aerated solution was slower at first, gradually increased to a maximum on about the ninth day, after which it progres-

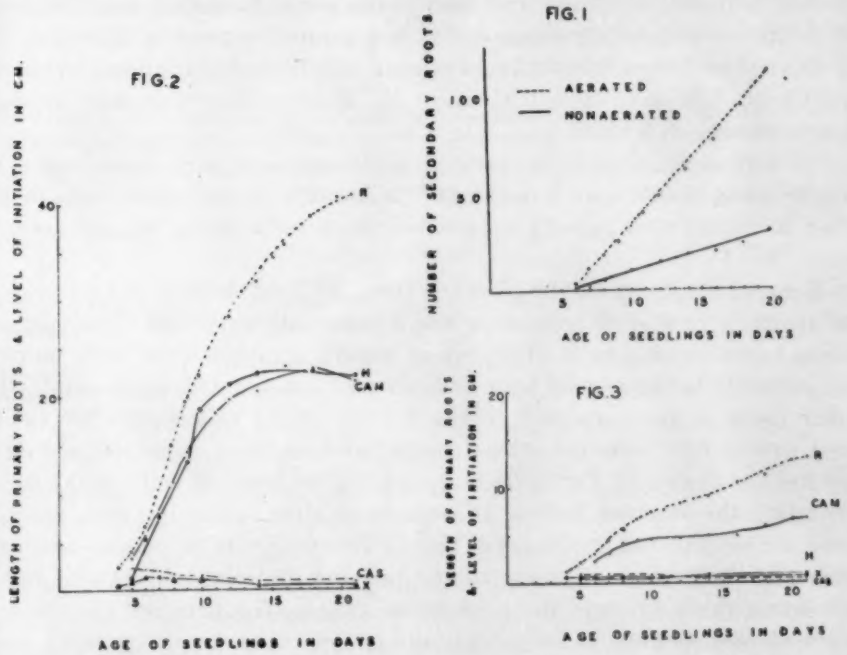

FIG. 1. Number of secondary roots on soybean plants cultured in aerated and non-aerated solutions. Each point represents the average of the number of roots found on 9 seedlings. FIG. 2. Length of primary root (R) and levels of initiation of vascular cambium (Cam), root hairs (H), Casparian strips (Cas), and lignification of protoxylem cells (X) in primary roots of different aged seedlings cultured in aerated solutions. Measurements were taken from the root tip. Each dot represents the average of the initiation levels in 5 to 7 plants, except that each dot represents the median length of 15 primary roots (R). FIG. 3. Length of primary root (R), and levels of initiation of vascular cambium (Cam), root hairs (H), Casparian strips (Cas), and lignification of protoxylem cells (X) in primary roots of different aged seedlings cultured in non-aerated solutions. Measurements were taken from the root tip. Each dot represents the average of the initiation levels in 5 to 7 plants, except that each dot represents the median length of 15 primary roots (R).

sively decreased. When the length of the root was plotted against the age of the seedling a sigmoid curve was obtained. Figures 2 (R) and 3 (R) illustrate the changes in the total length of the primary roots of soybeans cultured in aerated solutions, and in non-aerated solutions respectively.

A comparison of the two curves indicates that primary root growth was much retarded when plants were cultured in non-aerated solutions.

Roots of non-aerated plants, though shorter, were greater in diameter than those of aerated plants. In both aerated and non-aerated seedlings, root tips of younger plants were always greater in diameter than those of older plants. The diameter (1 cm. behind the root apex) of primary roots of 5-day-old seedlings[2] cultured in the aerated solution was 0.78 mm., while the corresponding diameter of non-aerated roots was 1.18 mm. In 14-day-old seedlings, root diameters at 1 cm. behind the apices were, respectively, 0.58 mm. and 0.91 mm. All these values represent average measurements of 9 roots.

In both aerated and non-aerated seedlings, secondary roots began to appear when plants were 5 days old. The number of secondary roots thereafter increased very rapidly on aerated roots, only slowly on non-aerated roots (fig. 1).

General structure of the primary root. At 1 cm. behind the root apex, the primary root of *Glycine max* has a uniseriate epidermis. The cortical parenchyma consists of 8–11 layers of loosely arranged cells with numerous intercellular spaces in both aerated and non-aerated roots, while the stelar tissue is more compact. The cell walls of the endodermis are thickened locally by Casparian strips. Immediately inward from the endodermis lies the pericycle. Pericycle is the outermost layer of cells of the stele, encircling the vascular tissues. It is procambial in origin but does not become a vascular tissue (Engard 1944). The pericycle is one to two cell layers in the regions adjacent to the primary phloem, and two to three cell layers thick opposite the protoxylem ridges. The primary phloem appears as four strands of cells lying alternately between the tetrarch primary xylem ridges.

Development of primary tissues. Primary phloem. During initial stages of phloem development frequent divisions occurred in incipient phloem regions of the procambium. Phloem strands were recognized by their cell arrangement, cell size, and location. They were located adjacent to the pericycle, alternating with xylem ridges and were composed of small cells which were arranged in semi-circular rows. Delimitation of primary phloem areas occurs 203 μ[3] behind the stelar initials in aerated roots and 200 μ behind the stelar initials in non-aerated roots (table 1).

The distance between the stelar initials and the first mature sieve tube element is almost the same for (1) roots which were cultured in the

[2] This and similar expressions of time will refer to the number of days following the time when soybean seeds, which had been soaked for 24 hrs., were first put into germination crocks.

[3] All the values which are referred to in the text hereafter, represent an average of a certain number of plants as in table 1 and 2.

aerated solution or in the non-aerated solution, and (2) roots of different ages. The level at which the first mature sieve tube element appears in any *one* of the four phloem areas is 410 μ behind the stelar initials in aerated roots and 423 μ in non-aerated roots. The levels at which a mature sieve tube element first occurs in all four of the phloem areas are 467 μ and 456 μ in aerated roots and non-aerated roots respectively (table 1, fig. 5). The levels of maturation of three sieve tubes in any *one* of the four phloem areas are 756 μ (aerated roots) and 698 μ (non-aerated roots) behind the stelar initials. The corresponding levels at which three mature sieve tubes

TABLE 1. *Levels of tissue delimitation and maturation (in* μ*) and lateral root initiation in aerated and non-aerated primary roots of soybean seedlings of different ages.*

Tissue	Aerated roots			Non-aerated roots		
	Range[5]	Average	No. of plants	Range[5]	Average	No. of plants
Pericycle delimitation	150– 182	163	26	150– 196	168	28
Phloem delimitation	190– 221	203	28	182– 221	200	29
Enlargement of metaxylem elements	190– 221	203	28	182– 221	200	29
Maturation of sieve tube elements[4]						
(a)	360– 492	410	30	351– 494	423	29
(b)	490– 570	467	29	377– 572	456	30
(c)	599– 996	756	29	469– 936	698	30
(d)	636–1224	886	27	661–1170	813	31
Lateral root initiation	1740–2028	1863	26	1760–2093	1871	21

are seen in each of the four phloem areas are 886 μ and 813 μ, in aerated and non-aerated roots respectively (table 1, fig. 6). These measurements indicate that the aeration did not affect the levels of differentiation and maturation of sieve tube elements.

Primary xylem. The acropetal development of the tetrarch primary xylem involves two distinct processes: 1) cell enlargement and vacuolation; 2) development of secondary wall and lignification. The vacuolation and enlargement of the xylem cells begins in the metaxylem and proceed

[4] Maturation of sieve tube elements:
(a) The level at which the first mature sieve tube element appears in any *one* of the four phloem areas.
(b) The level at which mature sieve tube elements first occur in each of the phloem areas.
(c) The level of maturation of 3 sieve tube elements in any *one* of the four phloem areas.
(d) The level of maturation of 3 sieve tube elements in each of the four phloem areas.

[5] These values represent the range of levels of tissue delimitation and maturation observed in roots of all plants of all ages studied. The measurements were made from the stelar initials.

centrifugally. Cell enlargement becomes evident in the metaxylem cells at about the same level as primary phloem delimitation (table 1, fig. 4). The development of secondary wall and lignification, on the other hand, begin in the protoxylem and proceed centripetally. The levels at which initial lignification of the protoxylem cells occurs in aerated and non-aerated roots are shown in figures 2 and 3 respectively. It will be noted that in primary roots which grew in non-aerated solution, the level of lignification did not vary too much with the age of the seedling, but remained within a range of 0.71 to 0.84 cm. from the root apex. In aerated roots, on

TABLE 2. *Levels (in cm.) of tissue differentiation and root hair initiation in aerated and non-aerated primary roots of soybean seedlings of different ages.*

Age of seedlings in days			5	7	10	14	21
Protoxylem lignification	Aerated root	Range[a]	0.80–1.30	1.50–1.64	1.00– 1.40	0.70– 0.75	0.50– 0.80
		Average	1.03	1.55	1.22	0.73	0.64
	Non-aerated root	Range[a]	0.80–0.94	0.70–0.85	0.70– 0.80	0.65– 0.80	0.70– 0.82
		Average	0.84	0.75	0.73	0.71	0.74
Casparian thickenings	Aerated root	Range[a]	2.00–2.53	1.80–2.25	1.20– 1.54	0.80– 1.22	0.70– 1.05
		Average	2.27	2.08	1.37	0.99	0.86
	Non-aerated root	Range[a]	0.80–1.20	0.80–0.23	0.80– 1.04	0.50– 0.71	0.50– 0.73
		Average	1.01	1.02	0.89	0.64	0.61
Root hairs	Aerated root	Range[a]	0.90–1.50	7.20–8.20	18.40–19.50	21.20–23.40	21.50–23.30
		Average	1.18	7.66	18.87	22.45	22.06
	Non-aerated root	Range[a]	0.40–0.80	0.40–0.90	0.70– 0.90	0.50– 1.20	0.90– 1.50
		Average	0.62	0.71	0.82	0.91	1.10
Vascular cambium	Aerated root	Range[a]	3.00–3.60	7.50–8.00	17.00–18.40	19.40–22.30	20.50–23.40
		Average	3.34	7.68	17.58	20.54	21.67
	Non-aerated root	Range[a]	no cambium	3.00–3.30	4.20– 5.00	4.60– 5.40	6.00– 7.50
		Average		3.12	4.58	5.04	6.80

the other hand, the level of lignification varied markedly with the age of the seedling. It changed rapidly from a point 0.79 cm. from the root apex in 4-day seedlings to a maximum of 1.55 cm. from the root apex in 7-day plants, and then gradually reverted, during the next two weeks, to a point about 0.73 cm. from the root apex (figs. 2 & 3, table 1). Lignification of the metaxylem cells was first noted on the 8th day in primary roots cultured in the aerated solution, and on the 10th day in those grown in the non-aerated solution.

Vascular cambium. Vascular cambium was first noted on the 4th day

[a] The values represent a range of 5 or more measurements for each age level. All measurements were made from the root tip.

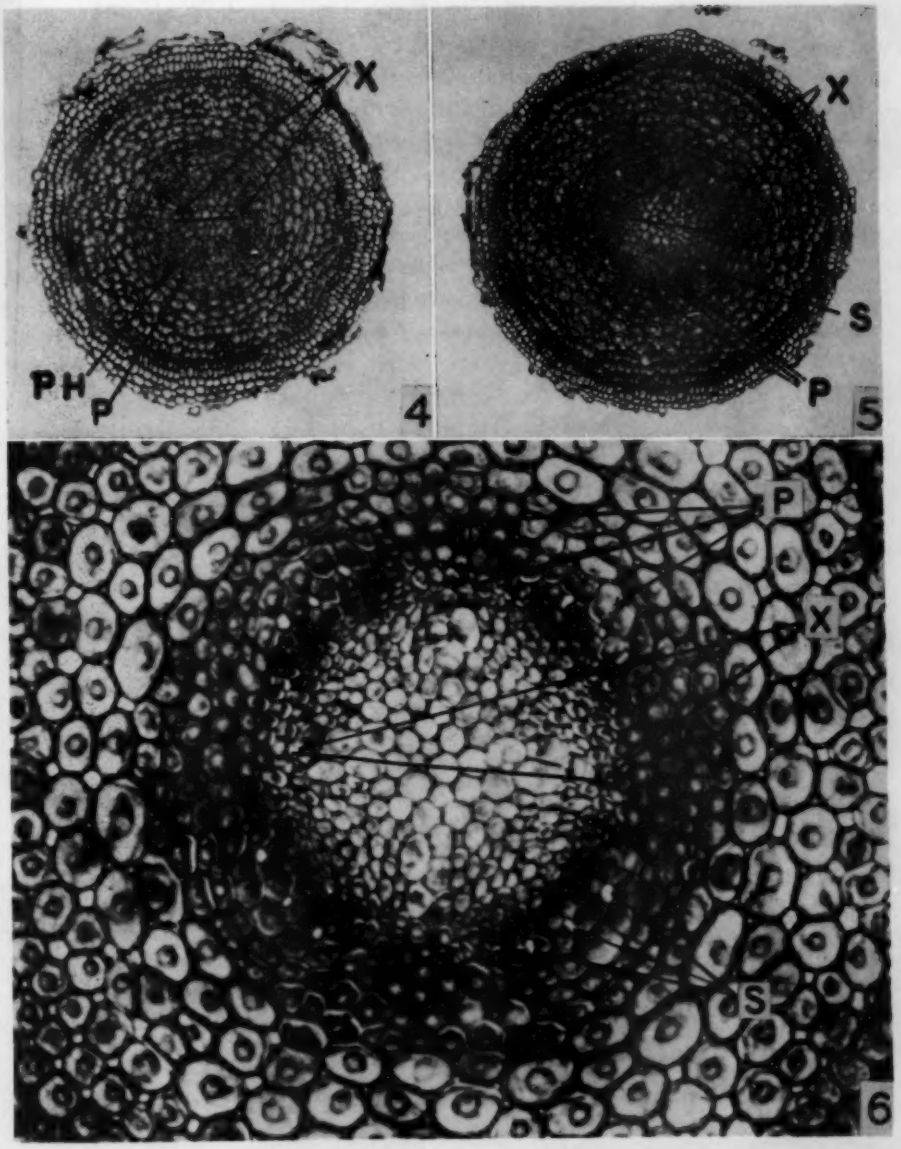

FIG. 4. Transverse section of a 7-day aerated root taken 240 microns behind the stelar initials. *p*, pericycle; *ph*, primary phloem; *x*, primary xylem. ×96. FIG. 5. Transverse section of a 7-day aerated root taken 492 microns behind the stelar initials. *p*, pericycle; *s*, sieve tube; *x*, primary xylem. ×88. FIG. 6. Transverse section of a 7-day aerated root taken 996 microns behind the stelar initials. *p*, pericycle; *s*, sieve tube; *x*, primary xylem. ×256.

in primary roots cultured in the aerated solution and on the 6th day in those cultured in the non-aerated solution. It first appears in the base of the root as separate bands of tangentially dividing cells. Each cambium strip originates from the dividing procambial cells situated at the inner edges of the phloem strands. From the beginning, it differentiates laterally and acropetally. Subsequently pericycle cells opposite the xylem ridges undergo periclinal divisions, forming bridges connecting the isolated vascular cambium (fig. 7). In aerated roots acropetal differentiation proceeds rapidly, while in non-aerated roots it is much retarded (table 2).

Pericycle. The pericycle becomes individualized at a distance of 163 μ (aerated roots) and 168 μ (non-aerated roots) behind the stelar initials (table 1). At levels of 410 μ (aerated roots) and 423 μ (non-aerated roots) behind the stelar initials, the pericycle cells begin to enlarge (fig. 5). At a distance of 756 μ (aerated roots) and 698 μ (non-aerated roots) behind the stelar initials, pericycle cells opposite the phloem strands become much larger than those opposite the protoxylem ridges and their cytoplasm becomes vacuolated (fig. 6).

Secondary roots arise in the pericycle at loci directly opposite the four protoxylem ridges (fig. 8). Thus the pattern of the primary structure of the main root determines the arrangement of the secondary roots in four longitudinal rows. Radial enlargement of pericycle cells adjacent to a xylem ridge is the first evidence of secondary root formation. This is followed by tangential and radial divisions of these pericycle cells. The cytoplasm of the dividing secondary root initials is very dense. The primordium continues to enlarge and elongate, forcing the epidermis and cortical tissues outward and eventually rupturing them.

Endodermis. Characteristic Casparian strips occur on the thin anticlinal walls of cells of the endodermis although they never become very thick. The level at which the Casparian strips appear is higher in aerated than in non-aerated roots, and in younger than older plants. The level of Casparian strip formation in 5-day aerated roots was 2.27 cm. from the tip as compared to a level of 1.01 cm. in non-aerated roots of the same age. In 14-day old seedlings the corresponding values were 0.99 cm. in aerated roots and 0.64 cm. in non-aerated roots (table 2).

Epidermis and root hairs. The epidermis is uniseriate. It consists of closely packed elongated cells with thin walls. Root hairs began to form on the fourth day. Roots cultured in the non-aerated solution produced an abundance of root hairs at levels approximately 0.62 cm. (5-day roots) and 1.10 cm. (21-day roots) behind the root tip. Root hairs of primary roots of soybean cultured in the aerated solution were sparsely developed except for certain regions at the base of the root (figs. 2 & 3, table 2).

Discussion. Soybean roots cultured in the aerated solution have a strik-

ingly different growth habit than those cultured in the same but non-aerated solution. The aerated roots were longer and smaller in diameter, thereby resembling the roots of barley (Bryant 1934). Abundant aeration favored increased branching of the soybean root system (Allison & Shive 1923, Loehwing 1934). On the contrary, non-aerated barley produced more roots than aerated ones (Bryant 1934). Bryant (1934) also found a considerable difference between the cortical parenchyma of aerated and that of non-aerated barley roots. The cortical parenchyma of aerated roots consists of uniformly compact cells with no conspicuous intercellular spaces, whereas the parenchyma of non-aerated roots is composed of widely separated narrow strands of cells. Similar results were found by McPherson

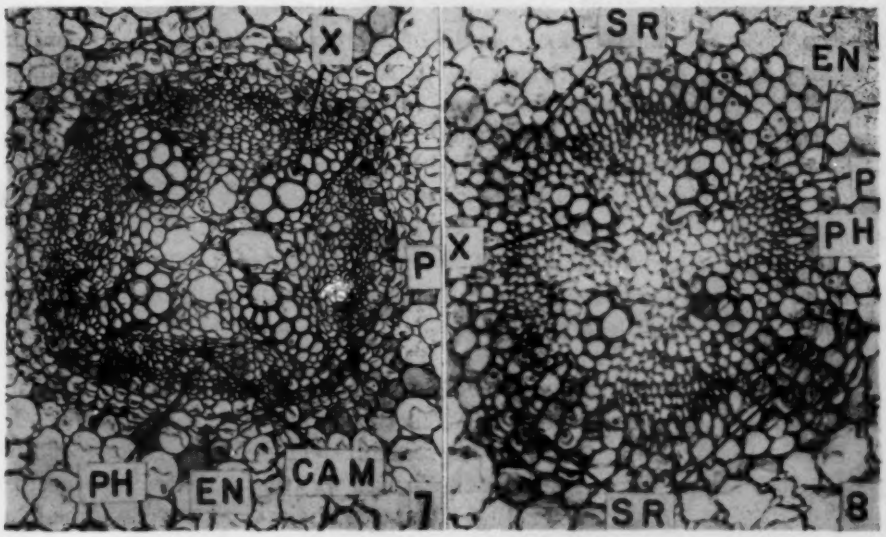

FIG. 7. Transverse section of a 6-day aerated root taken 6.3 cm. behind the stelar initials. *cam*, vascular cambium; *en*, endodermis; *p*, pericycle; *ph*, primary phloem; *x*, primary xylem. ×108. FIG. 8. Transverse section of an 8-day non-aerated root taken 7.5 mm. behind the stelar initials. *p*, pericycle; *ph*, primary phloem; *sr*, secondary root primordium; *x*, primary xylem. ×118.

(1939) in corn root. In the present work, however, no difference in the size of intercellular spaces in cortical parenchyma was noted. It might be concluded then that perhaps the plant responses to culture aeration vary with the degree of aeration as well as with the difference in species (Clements 1921, Clark & Shive 1932; Free 1917).

The differentiation and maturation of the xylem and phloem follow the procambium in its acropetal course (Esau 1940, 1943; Heimsch 1951). The aerated primary roots of soybean have the same pattern as do those non-aerated ones. In the soybean root, the first phloem elements mature closer to the stelar initials than the first xylem elements. The vacuolation

and enlargement of the xylem cells begin in the metaxylem and proceed centrifugally, whereas the development of secondary wall and lignification begin in the protoxylem and proceed centripetally. This conforms to the general differentiation pattern indicated by Esau (1954).

In barley roots (Heimsch 1951), relatively little variation occurs with respect to the levels at which vascular components are delimited, while extreme variations are found with respect to the levels at which the components mature. Heimsch also pointed out that the factors which directly determine the levels at which vascular tissue mature are more readily influenced by the developmental state of the root and are perhaps, independent from those which induce differentiation. In the present study of soybean, the levels of differentiation of pericycle, primary xylem and primary phloem, as well as maturation of sieve tube elements, are similar (1) for both aerated and non-aerated roots and (2) for roots of seedlings of different age. This similarity also exists for the level of initiation of secondary roots (table 1). The levels of initiation of xylem lignification, Casparian thickenings, root hairs, and vascular cambium differ not only (1) from aerated to non-aerated roots, but also (2) from young to old seedling roots (table 2).

An outstanding characteristic of the root epidermis is the development of root hairs. Ordinarily, the root hairs are confined to a region between one and several centimeters in length near the tip (Farr 1928). The actual development of root hairs is greatly affected by the environment (Cormack 1949). The more luxuriant growth of root hairs of soybean roots in the non-aerated solution corroborates a similar observation made by Snow (1905) on the roots of corn seedlings. The root hairs are usually interpreted as structures substantially increasing the absorbing surface of the roots (Farr 1928, Kramer 1945), but root hairs scarcely developed in the aerated soybean root. The roots developed in this environment perhaps absorb water through the epidermal cells. Rosene (1943) has demonstrated experimentally that hairless epidermal cells are capable of absorbing water.

SUMMARY

1. The root system of *Glycine max* consists of a primary root with numerous lateral roots, which are arranged in four longitudinal rows.

2. Primary roots of soybeans which are cultured in an aerated solution are several times as long as those cultured in a non-aerated solution, and the secondary roots are more numerous.

3. Root hairs of aerated primary roots are sparsely developed except along the basal portion of the root.

4. Roots cultured in the non-aerated solution produce an abundance of root hairs at a level of 0.8 cm. behind the root tip.

5. The levels of differentiation of pericycle, primary xylem, and primary phloem, as well as maturation of sieve tube elements, are similar and always below the level of Casparian thickenings (1) for both aerated and non-aerated roots and (2) for roots of different aged seedlings.

6. This similarity also exists for the level of initiation of secondary roots. In aerated roots, the level of vascular cambium and of root hair initiation are above the level of initiation of Casparian thickenings. In non-aerated roots, only vascular cambium initiates above the level of Casparian thickenings.

7. In seedling roots less than 12 days old, the levels of root hair initiation and xylem lignification are below the level of Casparian thickenings and in the seedling roots more than 12 days old, they are above the level.

8. Vacuolation and enlargement of xylem cells begin in the metaxylem and proceed centrifugally.

9. The development of secondary wall and lignification, on the other hand, begin in the protoxylem and proceed centripetally.

10. Vascular cambium appears first at the innermost edge of the primary phloem strands and develops laterally and acropetally.

11. It was first observed during the fourth day in primary roots cultured in the aerated solution and on the sixth day in those cultured in the non-aerated solution.

12. Secondary roots arise in the pericycle at loci directly outside the ridges of the tetrarch xylem.

I wish to thank Dr. R. A. Popham for his kind advice during the investigation. I wish to express my appreciation to Dr. B. S. Meyer for use of laboratory facilities.

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TORREYA

The Distribution of the Sand Hickory, Carya Pallida, in New Jersey

WAYNE E. MANNING

Carya pallida (Ashe) Engler & Graebner, a hickory primarily of the southern states, is not well known, nor is its distribution fully understood.

The sand or pale hickory is often confused with other hickories, especially the pignut hickories (*Carya glabra* (Mill.) Sweet and *C. ovalis* (Wang.) Sarg.), and the mockernut hickory (*C. tomentosa* Nutt.). It differs from the pignut hickories in having prominent tufts of hairs along many of the leaf rachises (rachis "villous"). It strongly resembles the mockernut hickory, an extremely common hickory in much of New Jersey, in this same feature, but differs from it in having the slender twigs and the lower surfaces of the 7–9 narrow leaflets, aside from the midribs, essentially glabrous. The lower surfaces of the young leaflets, the tips of the twigs, the buds, and the young fruits are silvery-scaly as well as golden-glandular. The fruit is not especially distinctive in itself, and ranges from a fruit with a rather thick (3–4 mm.), 3- to 4-valved husk to one with a thin husk (2 mm. thick), the fruit then strongly resembling that of the sweet pignut or red hickory, *Carya ovalis*. Keys to the species of Carya will be found in Manning (1950), Fernald (1950), Sargent (1933) and various books on trees. Sargent (1933) states that the mature terminal buds of the sand hickory are only about ¼" long (6 mm.), but on twigs of this species sent to the writer last winter from Tennessee some buds were 8–12 mm. long.

The names of hickories in many herbaria are rather confused, and the records reported here were made after most of the specimens of *Carya* were checked and rearranged.

Sargent and other authors report *C. pallida* in New Jersey only from the vicinity of Cape May, Cape May County. Studies of specimens from the herbaria of the Academy of Natural Sciences of Philadelphia, University of Pennsylvania, New York Botanical Garden, Rutgers University, and Bucknell University show that this species grows in at least seven of the southern counties. No record has been found for Pennsylvania, just across the Delaware River.

The localities at which this hickory has been found might be of interest, and are given below. It seems unnecessary to cite collectors' names and dates.

CAPE MAY COUNTY: Dennisville; East Creek; Marmora; 4 miles south of Ocean City, on Wildwood road; north of Palmermo; between Ocean City and Tuckahoe. CUMBERLAND COUNTY: 1 mile northeast of Dorchester; 1 mile west of Hoffman's Mill; Mannumuskin; south of Millville; 1 and 2 miles west of Vineland. SALEM COUNTY: 1 mile north of Jericho. ATLANTIC COUNTY: Bassett's Grove, Hammonton. GLOUCESTER COUNTY: Iona. CAMDEN COUNTY: Albion; Bishop's Bridge; 1¾ mile south of Kresson; West Deptford. BURLINGTON COUNTY: 1 mile west of Birmingham (about 4 miles east of Mt. Holly).

Although the sand hickory is probably uncommon and local, it must, of course, be more frequent than the records above indicate. The writer would appreciate seeing specimens collected in New Jersey and in other states.

Although Little (1953), basing his opinion according to a recent letter on Mattoon and Hawes (1926), cites *C. pallida* from Connecticut, and Gleason (1952) cites it from Massachusetts, the writer has so far not seen authentic specimens from these states. The species may occur there, or these records may be misidentifications based on hairy-leaved trees of the pignut hickories (*C. glabra* var. *hirsuta* or *C. ovalis* var. *mollis*: see Manning, 1950) or small-leaved trees of *C. tomentosa*. Thus, a recent letter from the New York Botanical Garden suggests that the Massachusetts record for the sand hickory in Gleason (1952) may be based on a mockernut hickory specimen from Dukes County, Mass. placed erroneously by someone in the *C. pallida* folder.

In the opinion of the writer Burlington County, New Jersey is, as far as the authenticated records show, the extreme northeastern extent of the range of this hickory.

In New Jersey this hickory occurs on the coastal plain. As Sargent (1933), Harrar and Harrar (1946) and others state, it extends south along the coastal plain of Delaware, Maryland, and Virginia, but further south it grows commonly on the piedmont. In Tennessee (Shanks, 1952) it grows in the Cumberlands, and East and West Rim, a part of the appalachian plateau province. In 1953 the writer collected this hickory on the Cumberland Plateau southwest of Knoxville.

Errors in distribution constantly creep into literature, as indicated above. Rehder (1934), for example, gives the distribution for *C. pallida* as only Ala. and Tenn. On the other hand the record cited by Deam (1940) at Vincennes, Knox County, Indiana, is not found in any of the common books on trees. The writer has seen the specimen collected by Deam, upon which this record is based, and agrees with Mr. E. J. Palmer in the identification. This is apparently the extreme northern limit for the species in the Central States.

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FIELD TRIP REPORTS

June 4. Mistaire Laboratories, Millburn, N. J. The American Fern Society and the Torrey Botanical Club met for an interesting full-day program comprising a symposium centered around fern spores and a visit to the Mistaire garden of over 80 native and cultivated fern species. Dr. Ralph C. Benedict, chairman of the meeting, introduced the five speakers taking part in the symposium. Another scheduled speaker, Dr. Norman P. Marengo, was ill, but later sent his complete text, summary, and photographs on "The Microscopic Structures of the Mature Spores of the Ostrich Fern, the Sensitive Fern, and the Royal Fern." Mrs. Lenette Rogers Atkinson described the triradiate spores of three species of *Anemia* (Schizaeaceae), and showed lantern slides to illustrate the lateral meristem of the gametophyte. Dr. Edgar T. Wherry outlined his theories on "Hybrid vs. Ancestral Ferns," using large charts to show *Dryopteris* relationships. Mrs. W. D. Diddell spoke on "The Spores and Sporangia of *Ceratopteris*," illustrating these interesting aquatic ferns with pressed herbarium specimens, photomicrographs, and projected microscope slides. Mr. F. Gordon Foster, discussing "The Microscopy of Fern Spores," demonstrated the correct use of the microscope and the effects of light and mounting media of varying refractive indices on spore detail.

A highlight of the program was the new SpeedMatic Micro-Projector loaned by Bausch and Lomb and demonstrated alternately by Mr. Foster and Mr. Burton Dezendorf of American Optical Company. This instrument showed spores and sporangia magnified up to 2350 × on a screen, illustrating Mrs. Diddel's *Ceratopteris*, and Mr. Foster's talk by showing *Osmunda* spores mounted in various media with the effects of different refractive indices on spore detail. These illustrations provided an excellent introduction to Miss Hires' subject.

Miss Hires spoke on "Three-Dimensional Fern Spores," summarizing her basic beliefs on spore shape and construction. Spore models, photomicrographs and drawings from the Mistaire collection added further support to her views, which differ from those generally accepted.

Miss Maud Mary Griswold of the Mistaire staff in "Models for Spore Study" stressed the value of models in learning and teaching about fern spores, and mentioned some of the technical and theoretical problems involved in model construction.

Interesting exhibits shown included Mr. Charles Neidorf's photographs of fertile fronds, beautiful drawings of the *Anemia* story from spore to prothallus and *Anemia* prothallia cultured by Mrs. Atkinson, and Mrs. Diddell's *Ceratopteris* specimens. The Mistaire exhibits included representative selections from the Mistaire collections of photomicrographs, models, herbarium specimens, and slides of fertile pinnae sealed between glass. This method of sealing preserves color and freshness of the specimens for at least a year if the slides are stored under refrigeration for later study. Attendance 47. Leader, Clara S. Hires.

June 18. Bayard Cutting Arboretum, Great River, Long Island. Mr. Henry Nye, Director, placed the facilities of the arboretum at our disposal. He called attention to the five well-marked trails, the latest one being the bald cypress trail which features a fifty foot specimen of *Taxodium distichum* Richard replete with pneumatophores. Trail #1 leads through the pinetum which contains mature specimens of several rare horticultural evergreens, notably *Sciadoptys verticillata*, *Cedrus atlantica glauca* Carriere, *Abies pinsapo glauca* Carriere, *Picea orientalis* Link, *P. abies gregoriana* Nash, *Taxus baccata stricta* Lawson. Many specimens have their lower branches layered in the humus.

The Wildflower trail leads around a series of dammed ponds. The vegetation is typical of pine barrens bogs except that white cedar is missing. Mr. Cutting has introduced some Southern plants, *Magnolia tripetala* L., Umbrella magnolia, and *Leucothoe Catesbaei* Gray, doghobble, which are becoming naturalized.

The bird watchers' trail follows the west bank of the Connetquot River, an estuarine inlet. Upland and shore birds were seen, including a pair of swans with two cygnets. Attendance 8. Leader, Robert B. Clark.

June 21–24. West Wardsboro, Vermont. The summer meeting of the Vermont Botanical Club attracted around 40 people of whom 12 at least were Torrey Club members. It was a delightful week for some who had arranged it as part of their vacation and arrived Monday for more leisure in the Green Mountain State. Many combined birding with botanizing and added new species as well as extraordinary views of familiar species to both lists. The several trips afield included visits to the varied habitats available: rocky woods, hillsides, open fields, marsh, bog, and pond. Out of this came a fern list of 28 species ranging from marsh fern through those of pasture and woodland to such lithophytes as rock polypody, blunt-lobed woodsia, wall rue, and the purple cliffbrake. We have no complete list of the seed plants seen but bogbean, twinflower, bunchberry, and Clintonia are representatives of the flora more northern than that of the Torrey Range. The leafy white orchis (*Habenaria dilatata*) was another such plant, new to some of our members. A list of 76 birds was turned in. Our thanks to T. B. C. and V. B. C. Member James Marvin, University of Vermont, for inviting us. Reported from notes of Barbara Cook.

June 26. Killingworth, Conn. We regret that none of our members took advantage of the Connecticut Botanical Society invitation to join this outing. Mr. Parent re-

ports that *Pogonia ophioglossoides* was seen by the thousands, making this one of the finest stations for the plant in New England. One pure white specimen was reported. "Better luck next time" concludes Mr. Parent. Thanks.

July 9. Binnewater Lakes region, Ulster County, N. Y. Joint meeting with the Eastern New York Botanical Club. The party first stopped at Forsyth Park in the city of Kingston to see a healthy stand of wall rue and cliff brake in crevices in Onondaga lime. Proceeding then to the Binnewater region in Hurley, they followed a woodland path thru glens and by a lake where limestone and shale alternate giving a very varied flora. A few of the more intersting plants were ginseng, opuntia, narrow-leaved spleenwort, Canada water-leaf, and broad beech, Clinton's, walking-leaved, and Goldie's ferns. Many interesting species of mosses and fungi were collected by members of the E.N.Y.B.C. Attendance 21. Leader, Henry F. Dunbar.

July 10. Iona Island, N. Y. Exploration of the fresh water swamp on this island was not attempted because of the excessive heat. Yet, on the swamp edge and on the knoll, a number of interesting plants were seen, at what the leader believes is their only station in the county. They were *Cheilanthes lanosa, Arisaema Stewardsonii, Habenaria clavellata, Xanthoxylum americanum, Ptelea trifoliata, Asclepias verticillata,* and *Campanula rotundifolia* forma *albiflora.* Attendance: Torrey 8, Rockland Audubon 6. Leader, J. Harry Lehr.

July 12. High Point State Park, New Jersey. Cumulative effects of three consecutive summers of drought reduced the number of species of plants in bloom at this season considerably. Mr. and Mrs. George Hallett have located a number of Botrychium stations near their home and were able to show the group *B. virgnianum, B. dissectum, B. matricariaefolium, B. lanceolatum,* and *B. simplex* as well as a large specimen of *Ophioglossum vulgatum. Epipactis Helleborine* was in flower nearby. A visit to a muskeg in late stage of development in Mashipacong Pine Swamp produced *Carex limosa, Woodwardia virginica, Kalmia polifolia, Andromeda glaucophylla,* and *Xyris montana.* Attendance 8. Leader, David Fables.

August 14. Many Swamps Trail, Rockland County, N. Y. The bogs were impenetrable after a two day record rainfall and the group limited its exploration to the border of Great Green Swamp. The leader believes this area contains the only county stations for *Woodwardia virginica, Eriophorum tenellum, E. virginicum, Rhynchospora alba,* and *Angelica venenosa.* These plants were all seen on this trip and in addition a second county station was found for *Viburnum cassinoides* and *Isotria verticillata.* Attendance: Torrey, 4; Rockland Audubon, 1. Leader, J. Harry Lehr.

BOOK REVIEWS

A Bibliography of Wisconsin Vegetation. By H. C. Greene and J. T. Curtis. 84 pp. Milwaukee Public Museum, Publications in Botany Number 1. 1955. $1.50.

Encompassing a period of nearly three centuries, 1667 to 1953, the Bibliography of Wisconsin Vegetation contains nearly a thousand entries. The scope of the bibliography, which is much broader than its title suggests, includes all publications and theses dealing with the distribution, taxonomy, ecology, sociology, economic uses, and conservation of the native plants and plant communities of Wisconsin. In addition, there are selected references from other fields which add peripheral information of value to students of Wisconsin vegetation. The most interesting of these supplementary sections is that which contains 71 references on the archaeology and ethnology of Wisconsin.

About 45 percent of the entries are annotated. The annotations, primarily geographical, are quite brief, often consisting of but one or two words. The titles are

chronologically arranged under 15 incoordinate subject headings: State floras, Regional floras, Taxonomic studies of vascular plants, Taxonomic, floristic, and ecologic studies of algae, of fungi, of bryophytes, Statewide vegetation studies, Regional vegetation studies, Paleoecology, Ethnobotany-archaeoecology-medical plants, General ecology, Forestry and conservation, Physical features of Wisconsin, Biographies of Wisconsin botanists, and Bibliographies which include references relating to Wisconsin material. An index permits reference to all the included titles by any particular author. Unfortunately, no index to the literature by political or natural subdivision of the state is included.

Several additional titles have been discovered since the bibliography went to press. These titles and titles of papers published since 1953 are being collected and will be contained in supplements to this bibliography which are to be issued from time to time. JACK MCCORMICK, In charge of vegetation studies, The American Museum of Natural History, New York 24, New York.

Weeds. By W. C. Muenscher. xvi + 560 pages, figs. 1–135, keys, glossary, literature references. MacMillan. 1955. $10.

Muenscher's "Weeds" has been an indispensable reference of those concerned with weeds and their control since the first edition appeared 20 years ago. Much information is presented concerning the source of weeds, their spread, their growth characteristics, and the losses which they cause. Methods for the control of weeds are also described. However, "Weeds" is probably best known as a guide to weed identification particularly of species common to northern U. S. and Canada. The second edition contains a key for the identification of 571 weeds with plates showing the entire plant or parts of 328. Species most easily confused are grouped in the plates. The nomenclature has been brought up-to-date. Muenscher has purposely omitted from the second edition any discussion of chemical control. This was done as it was recognized that chemical control today warrants much more detail than could be devoted to it in a book intended primarily for weed identification. Those concerned with weed identification will find this book a valuable tool. —R. J. ALDRICH, U. S. Department of Agriculture, and Farm Crops, College of Agriculture, Rutgers, the State University of New Jersey.

Handbook of Algae, With Special Reference to Tennessee and the Southeastern United States. By Herman Silva Forest. 467 pages, 2 sketch maps, 699 textfigures. (Contributions from the Botanical Laboratory, The University of Tennessee, N. Ser., no. 155.) The University of Tennessee Press, Knoxville. 1954.

Here is an attractively bound regional manual printed by the off-set method. A well constructed key to the genera occupies thirty-nine pages. Families, genera, and species are characterized in brief descriptions; and keys distinguish the species of the larger genera. Most of the species are illustrated with carefully executed drawings showing the essential morphological features. Although represented in the key to the genera, the diatoms are not treated among the species. A glossary of technical words and a short bibliography of general works on algae and of those dealing with the flora of the southeastern States conclude the book. The keys, descriptions, and comments on the species of *Ulothrix* and *Stigeoclonium*, which Dr. Forest has studied intensively for some years, will be of special scientific interest. The species of *Stichococcus* are included here among those of *Ulothrix;* on page 72, the new combination *U. bacillaris* (Näg.) Forest (= *Stichococcus bacillaris* Näg.) appears. Here and there typographical errors show themselves; the citations of authors of taxa and the references to the bibliography might well have been separated in the interest of precision. But these are matters of minor importance. On the whole, the book proves to be both usable and useful. —FRANCIS DROUET, Cryptogamic Herbarium, Chicago Natural History Museum.

Photosynthesis. By Robert Hill and C. P. Whittingham. viii + 165 pages. John Wiley & Sons, Inc., New York. 1955. $2.00.

Research in photosynthesis has been progressing so rapidly in recent years that the non-specialist has been hard put to keep up with the field. Rabinowitch's treatise has too much detail (and too high a price), while the ANNUAL REVIEW OF PLANT PHYSIOLOGY articles can cover only a part of the field each year. The latest of Methuen's Monographs on Biochemical Subjects is "an introduction to present researches in this field," with the emphasis on the biochemistry and physiology of photosynthesis. In 149 small pages of text the authors have done a fine job of bringing together the advances in a field which is of interest to all botanists.

The chapter on the structure of the plant in relation to photosynthesis emphasizes the role of diffusion and is somewhat scanty in its treatment of chloroplast structure. The chapter on photosynthetic pigments condenses into 25 pages the essence of these important compounds in a very straightforward fashion.

The remainder of the book deals with the physiological and biochemical aspects of photosynthesis, particularly with the fixation and reduction of carbon dioxide and the energy relationships of the reaction. The discussion leads up to the final chapter on the mechanism of photosynthesis which is a synthesis of present knowledge which will help the reader to follow and to understand subsequent developments in the field. The only disappointment is that the book was completed in early 1954 and thus does not contain more than tentative references to the rapid advances which the authors predicted in the closing paragraph.

There is only a brief number of references to the work mentioned in the book, and it must be remembered that it is just an introduction, but one which is a valuable addition to a biological library.

The *Methuen's Monographs* on biochemical and biological subjects have, in general, proved to be such handy little volumes that I would recommend to the publishers that a list of all the monographs be included in each volume.—CURTIS M. WILSON, Dept. of Plant Physiology, Rutgers, The State University of New Jersey.

Life Science. By Thomas S. Hall and Florence Moog. v + 502 pages. 487 illus. John Wiley & Sons, Inc., New York. 1955.

The authors, respectively Professor and Associate Professor of Zoology of Washington University, have presented material which is designed to give first-year students an adequate foundation in elementary biology. This material has been organized on the basis of physiological processes rather than on anatomical structure. Within each unit the basic historical experiments, upon which our modern concepts are based, have been presented in such a way that they emphasize the dependence of biological knowledge on experimental methods.

The unusual feature of the book is primarily its adaptability to different types of courses. The text, printed in type of two different sizes, contains sections in large type which would be satisfactory if used alone in a short course designed to give a general background to students who do not plan to major in the sciences. These sections would also be valuable on the reference shelves of a high school biology classroom. Sections in smaller type contain the more technical information. These might tempt the non-science majors to learn just a little more about those phases of the subject in which they become especially interested. A combination of both forms a complete course of elementary biology for science majors.

Basic chemical processes, essential to the understanding of those chemical processes which go on in plants and animals, have also been printed in small type. Although the authors have suggested that those students who are familiar with chemistry skip these sections, it would seem that the material is so condensed that it would be of more value as a review than as an introduction. A beginner in chemistry would need some elaboration by the instructor in order to fully understand these processes.

The book might possibly be used as a text if botany were given one semester and zoology the next, but the authors, both zoologists, have used a larger number of zoological illustrations of processes than botanical illustrations. This could introduce problems of enriching the work of the botanical semester and cutting some of the material from the zoological one.

Suggested experiments utilize materials commonly found in a well equipped laboratory. The explanations are clear and the text is not pedantic. An excellent list of references can be found at the end of each chapter. The authors have sometimes, unfortunately not always, included short summaries of the major points within a section.

The format makes the text easy to read. The paper is not too glossy and the pages are printed in double columns. The many line drawings are excellent, enabling the student to "see through" rather than to "look at" structures. They are refreshing as almost all are new and have been prepared to clarify this particular text. The photographs, most of which were taken by the well-known naturalist and nature photographer, Dr. Charles Schwartz, are both superior and essential. Certainly the book merits an examination by members of departments planning to introduce a new elementary biology text.—EUGENIA M. REID, Senior High School, New Brunswick, N. J.

Vascular Plants of Illinois. G. N. Jones, G. D. Fuller, and three collaborators. University of Illinois Press and Illinois State Museum. Urbana and Springfield, 1955. $10.

In April, 1945, there was published a Flora of Illinois, by George Neville Jones, in many respects a worthy addition to the series of our state floras. Later the same year this received in Rhodora a caustic review, with a "Supplement made from a desk-top in Massachusetts." In this supplement a number of records from more or less untrustworthy literature were exhumed and listed to suggest that the author of the Flora had not given attention to earlier work on the state's plants. In a rebuttal, however, the author was able to show that he had indeed checked many reports of taxa which seemed unlikely and had omitted those not supported by adequate specimens or other data. Additions and corrections were made in a second edition (1950).

The thoroughness with which Dr. Jones had reviewed the literature is now made evident by the publication of the Vascular Plants of Illinois, a 600-page quarto volume. This consists chiefly of a systematic list of the taxa known and reported from the state, with very full citations of works in which they have been discussed. For each taxon there are given references to the places of publication of the accepted epithets and pertinent synonyms and variants, the type localities, total ranges, and habitats within the state. For many taxa maps are furnished showing by dots the county occurrences. There are also supplementary discussions of the vegetation, lists of collectors, and full bibliography and index.

The book contains 18 nomenclatorial novelties, comprising one new species (*Aster chasei*), 11 new hybrids, 2 new combinations, and 4 changes in status.

For the most part the arrangement of the taxa is that of the familiar Engler-Prantl system, although there are a few unexplained shifts such as placing the Lauraceae after the Violaceae. Under each family the genera and the species are arranged alphabetically, a plan which so simplifies the finding of wanted epithets that it could well be more widely used.

Even though the editors of the current Gray (1950) and Britton & Brown (1952) both followed the International Code of Botanical Nomenclature, they did not always agree as to choice of epithets, so it seemed of interest to ascertain which usage the present work follows. Checking in systematic order a few of the conspicuous cases of divergence, the compilers of the present work prove to be largely independent. Thus, *Arisaema triphyllum* is interpreted as in B & B, but *A. pusillum* is accepted as a species. *Trillium gleasoni* (B & B) is preferred to the unidentifiable *T. flexipes* (G). *Habenaria bracteata* is kept as a species. In the use of *Quercus rubra* G is followed, but *Actaea alba* B & B *Aronia* appears as a genus, as in B & B. Our common Touch-me-not retains its American

epithet *biflora* (B & B) rather than the South African *capensis* (G). Differing from both works are such combinations as *Chimaphila corymbosa*, *Monotropa lanuginosa*, and *Pyrola americana*. The Fringed Loosestrife remains a *Lysimachia* as in G, the Green Milkweed an *Acerates* as in B & B.

The text matter is presented in 2-column plan, reproduced by an offset process from typewritten copy; the type-face is that used in ordinary printing, although the lines are not justified as could have been done on modern equipment. The stenographic work was unusually well-done, there being very few typographic errors. Even with the resulting economy in production, however, the price has had to be set at the high figure of $10 (though with an educational discount of $1). But even at this rate many taxonomists in regions far from Illinois are going to buy and use the book for its wealth of bibliographic data.—EDGAR T. WHERRY, University of Pennsylvania.

NOTE

Field trips with other clubs, either as their guest or as joint outings, have made this season's field schedule a very interesting one continuing a long established practice. We hope that the practice may continue and increase in its extent. Local clubs from anywhere offering field trips with plant study involved will favor us by extending an invitation. We have members all over the world and many of our members travel. They like to see the local flora. In return we shall be glad to have other clubs join us on trips that may be of interest to their membership. If such a club wishes a trip in the Torrey Range, 100 miles around New York, which is not already planned we shall try to arrange same jointly. Additional leaders and new objectives for trips are always desired too. Write to Dr. David Fairbrothers, Field Committee Chairman, Rutgers, The State University of New Jersey.—J. A. S.

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LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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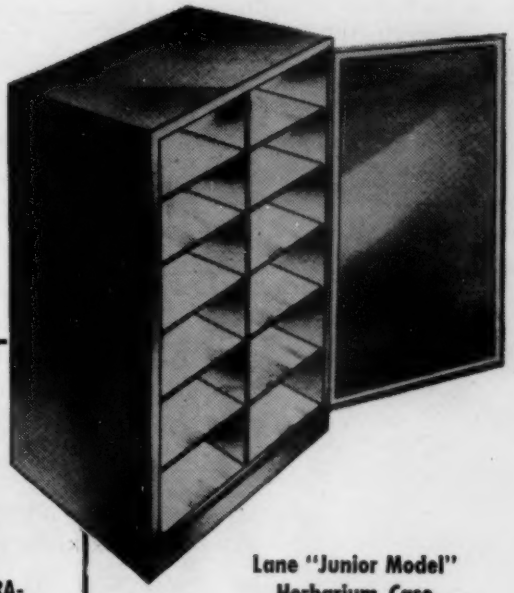

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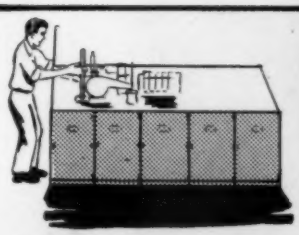

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